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The Amphibamidae (Amphibia: Temnospondyli), with a Description of a New Genus from the Upper Pennsylvanian of Kansas

Eleanor Daly

LAWRENCE

17 February 1994

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INTRODUCTION

A previously unknown Pennsylvanian dissorophoid is part of the fossil fauna of Hamilton Quarry, eastern Kansas (University of Kansas Vertebrate Paleontology KU-GRN-01); Greenwood County, ca. 2 mi E of Hamilton, (Sec. 5, T24S, R12E). The fossil-bearing limestone is a channel deposit in or has been eroded into the Topeka Limestone of the Shawnee Group, Virgilian Stage. Its relative time relations with other well-known Pennsylvanian vertebrate fossil localities are shown in Figure 1 (compiled from: Bell, 1944; Branson, 1962a, 1962b, 1962c; Carroll, 1967a, 1967b, 1969; Copeland, 1957; DeMar, 1970; Eagar, 1964; J. T. Gregory, 1950; Moran, 1952; Olson, 1946; Panchen and Walker, 1961; Peabody, 1952; Reisz, 1972; Romer, 1952; Vaughn, 1969, 1972; and Wanless, 1962).

Walter Lockard discovered the first vertebrate specimen, an acanthodian fish, at the quarry site in 1964 while looking for invertebrate fossils. In 1969, Thomas E. Bridge (Department of Geology of Emporia State University) began to take field parties to the quarry. Since then, fossil material from Hamilton Quarry has become more widely studied. The first published report was an abstract of a paper read at a Geological Society of America meeting (Bridge et al., 1972). In 1976, the fauna and flora of the quarry were the subject of a symposium at the 108th annual meeting of the Kansas Academy of Science (Trans. Kansas Acad. Sci. 79:99–102). In 1988, another Hamilton Quarry symposium was held at the 22nd annual meeting of the south-central section of the Geological Society of America, with a day-long field trip to the quarry area. The comprehensive field trip guidebook (Mapes and Mapes, 1988) is the best source of information on Hamilton Quarry and includes a complete history of work at the quarry (Bridge and Mapes, 1988).

The fauna reported from Hamilton Quarry includes tetrapods, acanthodian fish, sharks, lungfish, eurypterids, arachnids, insects, myriapods, crustaceans, bivalves, crinoids, bryozoans and fusilinids. By far the most common vertebrates are an acanthodian, *Acanthodes bridgei* (Zidek, 1976), and the labyrinthodont described herein. The fish remains often are whole bodies, and the tetrapods often are found as articulated groups of bones, sometimes as nearly complete skeletons. These specimens are either flattened onto a bedding plane in a layered brownish-gray to buff limestone, or preserved three dimensionally in a massive gray limestone.

THE HAMILTON LABYRINTHODONT

This labyrinthodont belongs to the Dissorophoidea, a group of rhachitomous temnospondyls known mainly from the Lower Permian of the south-central and southwestern United States. This superfamily is fairly well known, with more than 20 named genera. In general, dissorophoids are small to medium in size and their skeletons are well ossified overall with relatively long slim limbs and short vertebral columns. The interclavicles and clavicles of dissorophoids are small and their femora bear large adductor flanges. Typically, their skulls are short-faced with large orbits and high otic notches. Distinguishing marks of smaller scale are not lacking.

Initial assignment of the Hamilton labyrinthodont to a dissorophoid family did not present any problem. The gilled Micromelerpetontidae and Branchiosauridae (Boy, 1972) were clearly not nearest relatives. Of the terrestrial families, the Trematopidae were easily dismissed also. (The usual spelling of this family name, Trematopsidae, is not properly formed (from the genitive singular of the Greek *ops, opos*) and should be corrected according to the Code (Milner, 1978)). The Trematopidae are distinguished by antorbital openings that communicate with the external nares and by a somewhat squared snout (Berman et al., 1985). The Hamilton dissorophoid does not show these features. The best match was with the characters of the family Dissorophidae. Most notably, the squamosal of the Hamilton labyrinthodont bears a semilunar flange that projects ventrally into the otic notch (DeMar, 1968).

The dissorophids are best known for their dorsal dermal armor plates. Their skulls usually are ornamented with characteristic superficial ridges and exostoses. The Hamilton dissorophoid lacks these striking features, but they are lacking also in *Amphibamus* of the Pennsylvanian, *Tersomius* of the Lower Permian and *Micropholis* of the Lower Triassic, all heretofore considered dissorophids. These

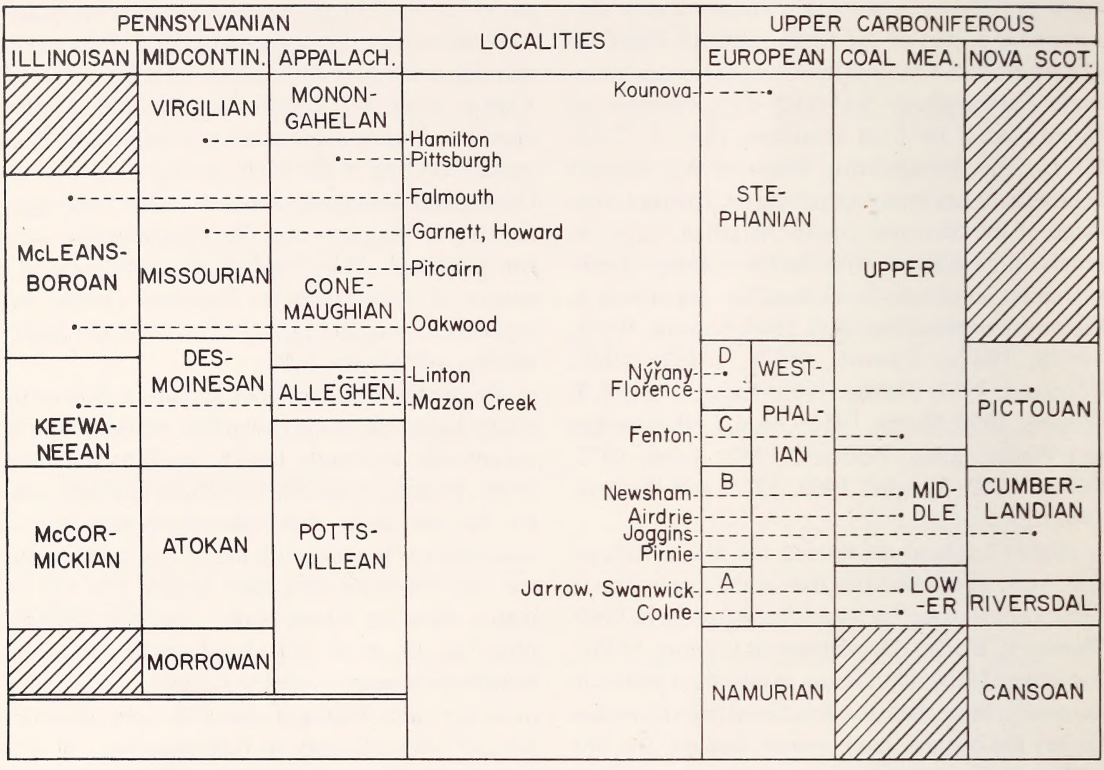

Fig. 1. Time relations chart of well-known fossil vertebrate localities of the Pennsylvanian and Upper Carboniferous.

unarmored, normal-skulled genera have always been placed at the base of proposed dissorophid phylogenies because of their apparently unspecialized nature and the great age of *Amphibamus* (Westphalian D equivalent).

Boy (1985) recommended removal of these atypical genera from the Dissorophidae, and suspicion is growing among other recent workers (Berman et al., 1987) that they cannot be included in any reasonable definition of the family. To test the idea that these unspecialized dissorophoids and the Hamilton dissorophoid are members of a long-lived distinct group, specimens of the North American *Amphibamus* and *Tersomius* species were assembled for reconsideration. As a result of this study and an extensive literature survey, this hypothesis is supported and familial reassignments are proposed.

ACKNOWLEDGMENTS

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ABBREVIATIONS

Used in figures:

F ..... frontal
J ..... jugal
L ..... lacrimal
MX ..... maxilla
N ..... nasal
P ..... parietal
PA ..... palatine
PF ..... postfrontal
PM ..... premaxilla
PO ..... postorbital
PP ..... postparietal
PR ..... prefrontal
Q ..... quadrate
QJ ..... quadratojugal
S ..... septomaxilla
SQ ..... squamosal
ST ..... supratemporal
T ..... tabular
V ..... vomer

Institutional acronyms are the following: American Museum of Natural History (AMNH), Field Museum of Natural History, University of Chicago (FMNH UC or UR), Emporia State University (HQ), Museum of Natural History, The University of Kansas (KUVP), Museum of Comparative Zoology (MCZ), University of California at Los Angeles (UCLA VP), United States National Museum of Natural History (USNM), and Yale Peabody Museum (YPM).

SYSTEMATIC PALEONTOLOGY

Class Amphibia
Order Temnospondyli
Superfamily Dissorophoidea
Family Amphibamidae

Type genus.—*Amphibamus* Cope 1865.

Revised diagnosis.—Dissorophoid temnospondyls, distinguished as follows:

1. Pleurocentra extend ventrally to meet, or almost meet, below the notochord;
2. Ribs short posterior to the shoulder region, such that the rib series lacks a thoracic basket.

In addition to these apomorphic characters, a constellation of primitive ones is usually present, as follows: small external nares, stapedial foramen, moveable basal articulation of the braincase, iliac blades curving posteriorly, overlapping bony scales.

The short ribs of amphibamids are distinct from those of trematopids in that they are not flattened or overlapping in the thoracic region (Williston, 1909; Case, 1911). The reduced axial rib pair of branchiosaurs (Boy, 1978) is absent in amphibamids.

Taxonomic note.—Peliontidae Cope 1875 is the oldest family name attached to the type genus. The combination *Pelion lyelli* was created by Cope (1868) for Wyman's (1858) *Raniceps lyelli* because the generic name was preoccupied, and he created the family name soon after. *Pelion* Cope 1868 is a junior homonym of *Pelion* Kirby 1858. According to Article 39 of the Code, a family name is invalid if the name of its type genus is a junior homonym, so Peliontidae should be replaced. The family name Amphibamidae Moodie 1910 is used instead.

Eoscopus, new genus

Etymology.—From Greek *eo* "dawn" and *skopos* "watcher."

Diagnosis.—Amphibamid dissorophoid with a relatively narrow interorbital bridge; eight pairs of shoulder ribs that begin on the axis, with the first five pairs more robust; a single spatulate pair of sacral ribs; a deep contact between pelvis halves for the anterior two thirds of their length, followed by an interdigitation; terminal phalanges knobbed.

Eoscopus lockardi, new species

Named in honor of Walter Lockard.

Diagnosis as above.

Taxonomic note.—This name was published in Daly (1976) without a taxonomic description, thereby creating a *nomen nudum*. The correct date of publication is therefore that of this paper.

Holotype.—KUVP 80408. Skull and anterior vertebrae, part and counterpart (Fig. 2).

Paratypes.—Listed below. All skulls are dorsoventrally flattened and split through the dorsal bones unless otherwise indicated.

KUVP 47270. Posterior dorsal part of a skull and a long series of vertebrae.

KUVP 47272. Skull fragment, including a set of circumorbital bones and a palpebral cup.

KUVP 49491. Presacral vertebral column, pelvis, and femur.

KUVP 50000. Premaxilla and maxilla.

KUVP 80409. Skull and anterior vertebrae.

KUVP 80411. Skull, presacral vertebral column, girdles, and femora.

KUVP 80412. Posterior part of whole animal, with tail and lower part of one leg missing.

KUVP 80413. Skull, part and counterpart.

HQ 14. Partial skull, including orbits and anterior portion.

HQ 15. Partial skull, lacking part of right side.

HQ 122A–B. Skull and anterior vertebrae, part and counterpart.

HQ 123A–B. Pelvis and one hind leg, part and counterpart.

HQ 127. Half pelvis and one hind leg.

HQ 247. Pelvis of young individual (pubes lacking).

HQ 250A–B, D–I. A largely complete specimen, preserved in the round. Most of the skull and tail are missing, as well as the distal part of one hind leg, the interclavicle, and cleithrum.

HQ 252. This specimen is the counterpart of KUVP 80412.

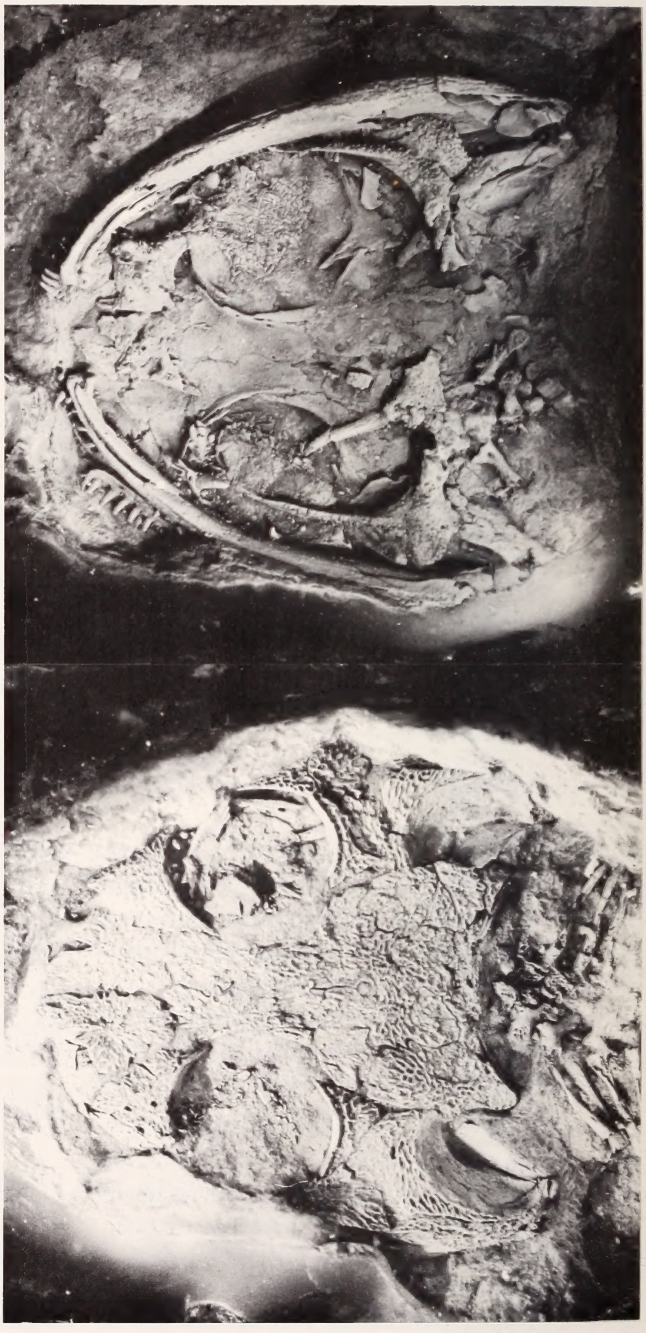

Fig. 2. *Eoscopus lockardi*, gen. et sp. nov. The holotype, part and counterpart, × 1.5. KUVP 80408A is at the top and KUVP 80408B is at the bottom.

HQ 254A–B. Partial foot, part and counterpart.
HQ 255B. Partial skull, posterior half.
HQ 258A–B. Skull, part and counterpart.
HQ 260. Skull.
HQ 424A–B, HQ 428. Partial skull, some vertebrae and limb bones.
HQ 431. Vertebrae, ribs, femur, tibia, and fibula.
HQ 551A–C. Nearly complete skeleton with partial body shadow, some scale impressions, and dark eyeball remains; part and counterpart.
HQ 598A–D; HQ 599A–D. Partial skeleton, including a laterally compressed skull, vertebrae in line, and scattered limb bones.
HQ 641. Scapulocoracoid and humerus.
HQ 716A–B. Partial skull, part and counterpart.
HQ 720. Disrupted skull and complete vertebral column.

Description

General features.—The size and proportions of *Eoscopus* are easily observed in specimen HQ 551A, B, and C (the poorly preserved remains of a nearly whole animal). The head of HQ 551 is nearly half as long as the trunk (3.5–7.5 cm). The head of HQ 598 and 599 is two-fifths the length of the trunk (3.5 to 8.5–9.0 cm). This is also the proportion of KUVP 80411 (3.3–7.5 cm).

The tail of HQ 551 can be seen on part B as an impression on the stone, when the light is almost parallel to the surface. It is estimated to have been 5.7 cm long when complete, about three fourths as long as head and body together. Individual HQ 252-KUVP 80412 has both trunk and tail; the tail is about four fifths as long as the trunk (6.3–7.5 cm).

The hindlimb of HQ 551 is approximately 4.5 cm long (three fifths of trunk length), and that of HQ 252-KUVP 80412 is about 5 cm long (two thirds of trunk length). It seems that the individual with a longer tail also has longer limbs. HQ 250, a larger animal with a trunk 12–13 cm long, has a hindlimb that is three fifths of trunk length. The humerus of HQ 250 is essentially the same length as the femora (2.6, 2.7 cm), and its ulna is the same length as the tibia (1.6 cm), but the radius is shorter (1.4 cm). In general the proportions of the limb segments are primitive; thus the distal parts are shorter than the proximal ones and the radius is 0.54 of the length of the humerus (Hotton, 1970).

Scale impressions are faintly visible in the darkened areas around some of the bones of HQ 551. Apparently *Eoscopus* was completely covered in overlapping, rounded scales, arranged in vertical rows around the body. They are clearest at the wrists and ankles, which are unossified in this individual. No dermal armor or ossicles have been found associated with any specimen, except in the eyelids and palate.

Some of the specimens were prepared for study by embedding them in plastic and removing all of the matrix with 10% acetic acid. After this treatment, it was possible to see the internal structure of the long bones and the neural arches, because the articular surfaces were cartilaginous. The interior of the round bones is filled with a meshwork of bony tubules.

Skull.—Nearly all of the skull specimens are flattened dorsoventrally; those that are preserved in the round are fragmentary. The dermal bone pattern is shown in the reconstruction (Fig. 3). Measurements were made of the distance from the ventral edge of the quadratojugal to the lateral edge of the supratemporal to approximate the greatest height of the skull. This distance is about one fourth to one third of the midline length, indicating a rather low skull. Skull measurements are presented in Table 1.

Because the bones are split in most Hamilton specimens, the outer surfaces must be observed on the acid-prepared skulls KUVP 80408 and KUVP 47270. *Eoscopus* possesses the usual ridge-and-pit surface ornamentation of the outer skull bones. Lateral line canals are absent, as are the ridges and exostoses seen on the skulls of most dissorophids. The sutures are unfused.

The most noticeable feature of these skulls is the relatively large size of the orbits, and the accompanying narrowness of the interorbital bridge. Orbit length varies from 0.30–0.42 of the total length in the midline of the skull. There does not seem to be any associated trend with increase in size. A ridge, borne on the prefrontal, frontal, postfrontal, and postorbital bones borders each orbit around the medial half of its circumference.

The eyes of *Eoscopus* were covered with large palpebral cups, composed of a mosaic of small, cornered pieces of bone (KUVP 80413). The intact cups closely approximate the prefrontals, frontals,

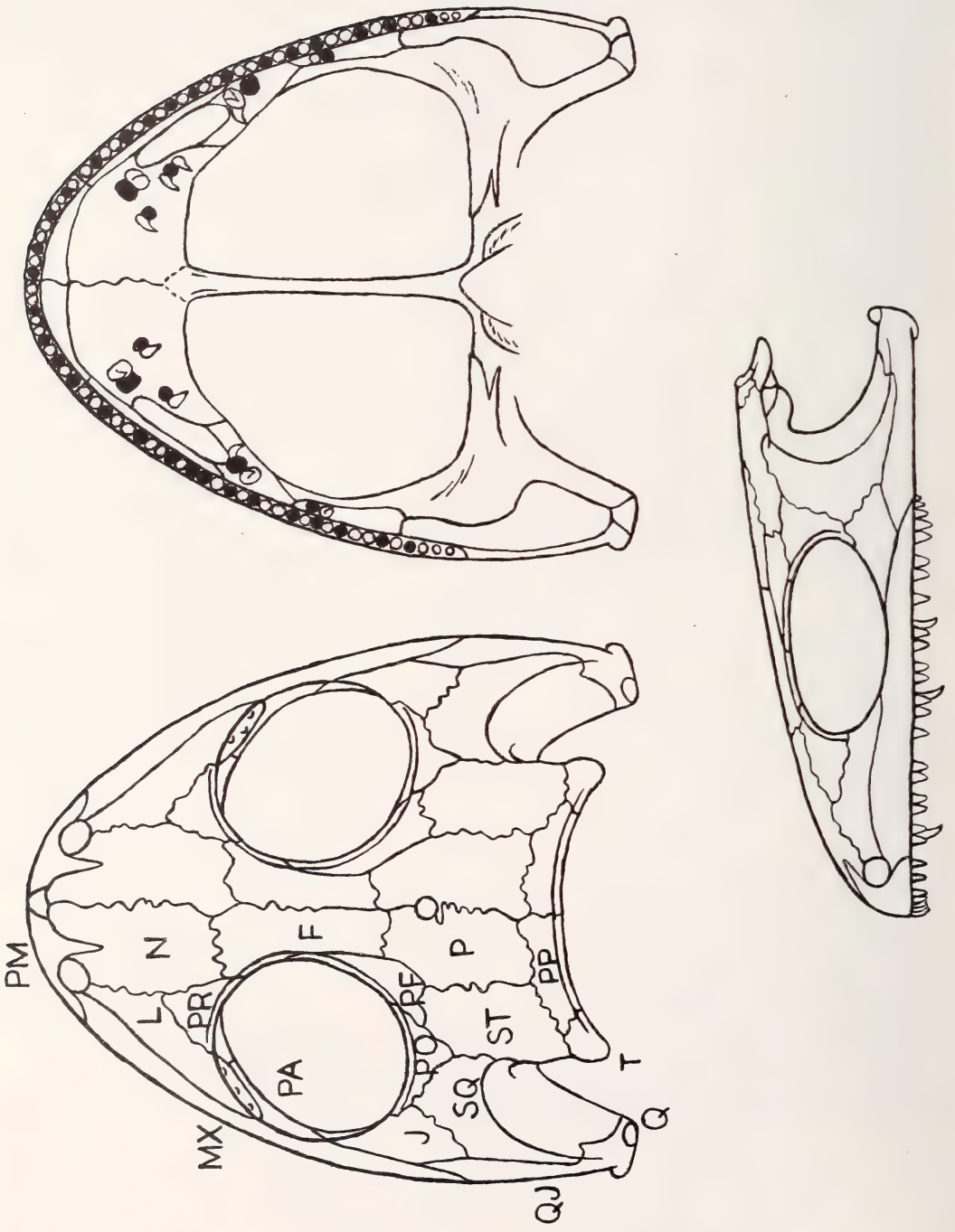

Fig. 3. *Eoscopus lockardi*, gen. et sp. nov. Reconstruction of the skull in dorsal, ventral and lateral view, ×2.

Table 1. Selected skull measurements of *Eoscopus lockardi* in cm.

Specimen number	Skull length	Muzzle length	Orbit length	Table length	Bridge width	Table width	Skull height	Postorb. bar length	Height/ length
KUVP 47270	—	—	—	—	1.41	3.35	2.0	—	—
KUVP 80408	3.35	1.0	1.2	1.35	0.65	1.85	1.05	0.75	0.28
KUVP 80409	3.8	1.4	1.4	—	0.42	—	—	—	—
KUVP 80411	3.3	1.06	1.3	0.85 1.28	0.54	1.93 2.42	0.95	0.45	0.29
KUVP 80413	3.65	1.1	1.45	1.1	0.65	2.05	1.05	0.6	0.29
HQ 14	—	1.2	1.6	—	0.57	—	—	—	—
HQ 15	5.55	2.0	2.0	1.8	1.25	—	1.5 est.	1.0	0.27
HQ 122	3.8	1.1	1.6	1.2	0.62	2.25	1.0	0.7	0.26
HQ 258	3.5	1.1	1.0	1.25	0.5	—	—	0.75	—
HQ 260	3.85	1.15	1.45	1.15	0.6	2.05	1.0	0.65	0.26
HQ 598–599	3.4	1.35	0.95	0.95	0.45	—	0.7	0.65	0.21

and postfrontals and leave a crescentic area uncovered on the lateral side of each orbit. Many other specimens have partially preserved cups, and in all cases the bony pieces have the same size and shape.

Ocular plates were present in the eyeballs (KUVP 47272 and HQ 551). It is not possible to say how many made up a complete ring but 15 plates is the minimum (KUVP 47272).

The infilling of the canal is a prominent marker of the lacrimal bone in many specimens. The foramina of the orbital surface are preserved only on KUVP 80408. This acid-prepared specimen shows three foramina in each orbit, arranged linearly on the left lacrimal and triangularly on the right. The contact between the prefrontal and the palatine expected in a dissorophoid is internal to the orbital surface of the lacrimal. For confirmation of this, it is possible to observe the size and shape of the disarticulated palatine in the right orbit of KUVP 80408. The dorsal part of the palatine extends from a short rostral process of the prefrontal to contact the jugal at the midventral border of the orbit. The external exposure of the palatine probably is confined to the anteroventral rim of the orbit. There is no external exposure of the ectopterygoid. HQ 14, 122A, and 258B have the bones of this area in articulation.

In the intact skull there is sometimes a definite cornering anterodorsal to each orbit, as the roof passes from top to side. This, together with its inturning into the front wall of the orbit, gives the prefrontal an inflated appearance in some cases. In some specimens the prefrontal is only slightly curved, whereas in others it is cupped. It is best observed on HQ 14, 122A, and KUVP 80408 and 80413. Another visible cornering usually is present at the anterior apex of the otic notch, between the skull table and the cheek.

The external nares are observable only on HQ 258B. They are small and anterolateral in position. On all other skulls they are concealed or obliterated by displacement of the surrounding bones. The septomaxilla is not observable on any specimen. A rostral fontanelle, bounded by the nasals and premaxillae, is present between the nares. This feature is best viewed on HQ 14, 15, and 260.

The dorsal processes of the premaxillae are long and close to the nares. They fit into notches in the nasals, which are floored with bone. As a result, the dorsal processes cannot be viewed without removing some of the nasal bone ventral to them. HQ 14 and 260 were prepared to expose the processes. The notch medial to each naris is a feature of the nasal and is exposed on KUVP 80408. It can be seen in outline on HQ 14 and 551C.

An internal nasal flange was discovered in a few other dissorophoids (Bolt, 1974a). It is present in *Eoscopus* and is partially preserved on KUVP 80408, where it can be seen through a gap in the anterior portion of the palate. On the ventral surface of the nasal bone, the long flange extends anteromedially from the apex of the prefrontal. A posterior part of the flange extends along the anteroventral edge of the prefrontal from the anterior corner to the curve near the orbit. The flange may include a lacrimal

contribution, but the ventral surface of the lacrimal bone is not preserved on KUVP 80408.

The otic notch is large, as expected for dissorophoids, curving concavely ventrally from an anterior apex. A supratympanic flange is present, but is preserved only on KUVP 47270 and HQ 598A. Its ventral edge has a squamosal semilunar flange, typical of dissorophids (DeMar, 1968). A supratympanic shelf (Bolt, 1974c) extends from the skull table above the supratympanic flange. The area ventral to the shelf is unsculptured, as in trematopids (Berman et al., 1985) and (apparently) *Iratusaurus* (Gubin, 1980). Ventral to the shelf, near the end of the skull table, the supratemporal bears a ventral projection, a semilunar flange (Bolt, 1974c). There is a tabular contribution to the supratympanic flange also. It is difficult to determine whether the squamosal has a small contact with it or not.

Only KUVP 80408 shows the condylar area well. The subotic parts of the squamosal and quadratojugal completely cover the posterior portion of the quadrate. They are delimited from the lateral sculptured parts by a definite rim. The posteromedial process of the quadratojugal nearly encircles the dorsal process of the quadrate. The lateral portion of the condylar surface is borne by the quadratojugal cover in *Eoscopus*. The dorsal process of the quadrate is a strong knob, wider than long, with a rounded top.

Eoscopus possesses short tabular horns, which vary somewhat in shape and angle and can be seen on KUVP 47270, 80408, and 80413, and HQ 15 and 598A. The horns turn slightly ventrally from the plane of the skull table. On KUVP 80408 the horn has a light pitting on its outer side, rather than normal sculpturing. This is not true of KUVP 47270, another acid-prepared specimen.

The round parietal foramen is always present a short distance behind the orbits. This opening lacks a raised rim. The posterior border of the skull table is marked by a grooved ridge running from side to side. The occipital cover is not well preserved on any specimen. Some of it seems to be present on KUVP 80413 and HQ 15. A sheet of dermal bone probably extends to the foramen magnum and ventrally on both sides as two lobes, and then shortens laterally until it disappears into the skull table again at about the middle of the tabulars. The ventral surface of the dorsal part of the postparietals are exposed on HQ 250A. A round hole, located somewhat laterally, occurs in each bone. The holes may represent rugose attachment areas that were pulled off when HQ 250 was split into its parts.

The marginal teeth are large and curve inward at the tips. Broken teeth have thin walls and large pulp spaces. Externally, labyrinthine grooving seldom is visible, but when larger teeth are chipped, ridges on their inner walls leave vertical stripes of dentine on the matrix infilling. Size and spacing of teeth is similar in upper and lower jaws. Counts of teeth and tooth spaces of selected upper jaws are presented in Table 2. Countable upper jaws of *Eoscopus* possess 40–65 teeth; the number varies with the length of the bones.

The palatal view of the skull is dominated by the large interpterygoidal vacuities. Braincase bones cannot be seen through them, or posterior to the parasphenoid; these bones were unossified in all specimens. The bones surrounding the vacuities are covered with large curved denticles, and the vacuities themselves were covered with denticulated skin. The denticles are borne in small groups on bony platelets (HQ 15). The palpebral cup ossicles can be distinguished from the palatal platelets by shape: palpebral cup bones are cornered, whereas palatal platelets usually are larger and more rounded. A similar covering for the vacuities has been reported for the dissorophids *Broiliellus hektotopos* (Berman and Berman, 1975) and *Kamacops acervalis* (Gubin, 1980). Steen (1931) found them on *Amphibamus lyelli* and *Stegops divaricata,* and Romer (1930) described them on *Erpetosaurus,* a colosteid.

Fang-and-pit pairs are present in the positions typical of temnospondyls. The best prepared vomers, on KUVP 80408, are patchily set with strong recurved denticles, which point toward the posteromedial corners of the bones. There are three pairs of fangs-and-pits on the right vomer and four on the left. The largest fang is located at the anterior end of the internal naris. Its recurved tip points posteriorly. Another occurs on the medial border of the naris. On the left vomer, another smaller fang is located on the border just posterior to it. The remaining fang lies in the middle of each vomer, between the naris and the midline of the palate. The smaller fangs are not as erect as the one at the end of the naris, and they are slightly more curved and point strongly in the same direction as the denticles.

The palatal pattern of KUVP 80409, a second

Table 2. Measurements in cm and tooth counts of upper jaw bones of *Eoscopus lockardi*. Left above, right below.

Specimen number	Premaxilla length	Premaxilla count	Maxilla length	Maxilla count
KUVP 50000	1.32	21	4.89	44
KUVP 80408	0.71	11	—	—
	0.79	12	—	—
KUVP 80409	0.80	12	not	35
	0.81	12	measurable	33?
KUVP 80413	0.74	12	2.62	32
HQ 14	0.70	10	2.85	30
	0.76	10	incomplete	30
HQ 15	1.13	16	4.23	44
HQ 122 A	0.70	10	2.86	34
	0.75	13	2.82	36

acid-prepared specimen, is somewhat different (Fig. 4). Only the fangs at the anterior ends of the internal nares are present. The remainder of the vomers is covered with a uniform carpet of denticles, so that it is certain that other fangs were absent. Either there is a great deal of individual variation in vomerine dentition, or some kind of polymorphism is present. It is possible that this specimen might represent another amphibamid taxon; however, it differs from KUVP 80408 only in this character.

A large palatine fang-and-pit present at the posterior end of each naris is comparable in size to the anterior set. The tip of this fang points posteromedially. On KUVP 80408, a small fang is located medial to this larger one, but this is not the case with KUVP 80409. Like the palatine, the ectopterygoid bears a fang, the tip of which points posteromedially.

The exact shape of the vomers is not preserved because of breakage anteriorly and posteriorly. Nevertheless, most of the vomer is visible. Posterior to the transverse posterior borders of the premaxillae is a rounded, denticle-free space. This probably is the internarial pit found in some other dissorophoids and which is flattened into the plane of the rest of the palate in both of these acid-prepared specimens. No internarial foramen has been observed on these specimens.

Both the upper and lower sides of the ectopterygoid are observable on KUVP 80408. The contacts of its anterior end are visible on KUVP 80413. On the palatal surface a wide smooth groove extends anteriorly from the posterior edge and to an elongate foramen. In dorsal view, the foramen is larger and rounder than in ventral view, and an anteroposterior in-

Fig. 4. *Eoscopus lockardi*, gen. et sp. nov. The palate as seen on KUVP 80409, × 2.

ternal divider is visible. The medial border of the pterygoid is thickened, so that the interpterygoidal vacuity is rimmed with a prominent heavily denticulated ridge for about half its length. The ridge is low anteriorly, but enlarges posteriorly and finally transforms into the round, hollow projection of the internal process of the pterygoid. The denticles that cover the ridge continue onto this process for most of its length and pass posteriorly onto the quadrate ramus also. On KUVP 80408, denticles exist only near the internal process, but on 80409, they extend halfway to the squamosal contact.

The internal processes of the pterygoid are preserved on KUVP 80408, 80409 and 80413. Their open ends are confluent with V-shaped openings in the posteroventral sides of each process. In life, the pterygoid shells covered cores of palatoquadrate cartilage. A similar morphology was described for the dissorophid *Ecolsonia* (Berman et al., 1985), which has an ossified braincase. In this animal, a triangular posteroventral part of the basipterygoid process fits into the V-slot of the internal process of the pterygoid.

For the lateral half of its length, each internal process of the pterygoid is attached to the convex anterior portion of a dorsoventrally compressed lamina ascendens. This transverse sheet of bone, that normally is oriented vertically, is now curled due to flattening of the skull. Laterally it merges with the quadrate ramus just above the internal process of the pterygoid, while its free end extends a little further medially than the process.

An epipterygoid is present in the left interpterygoidal vacuity of KUVP 80408, lying lengthwise. It consists of a conical base, unossified ventrally, and a strong ascending process. The epipterygoid ossification could not have participated in the lateral side of the basal articulation, because the pterygoid completely surrounds that part of the palatoquadrate.

The most prominent feature of the parasphenoid is its elevated, triangular denticle patch at the base of the rostrum. This area is preserved on KUVP 80408 and KUVP 80409, along with most of the rostrum. The apex of the triangular denticle patch projects well below the palate. From there the surface slopes posteriorly and at its base, bends to the level of the rest of the parasphenoid. Recurved denticles carpet this triangular area closely and uniformly. The two foramina for the internal carotid arteries are in the lateral faces of the denticle platform. They are invisible ventrally because the edges of the triangular area are laterally produced. On KUVP 80409, shallow grooves can be seen curving medially to approach the foramina at a 45° angle.

Most of the slender parasphenoidal rostrum is present on KUVP 80409. As it approaches the vomers, two narrow ridges rise along its sides, creating a shallow ventral trough. The rostrum probably widens where it contacts the vomers. The anterior corners of the posterior plate are everted and convex, while the transverse anterior edge remains straight. Each protrusion once covered the posterior and ventral sides of a cartilaginous basipterygoid process. Unfortunately the posterior parts of the parasphenoid are not well preserved.

A stapes is approximately in position on the right side of the parasphenoid of KUVP 80408. It is a robust, perforated rod with an enlarged proximal portion. A second stapes lies inside the curve of the lamina ascendens on the left. Its unfinished footplate shows its tubular interior structure. KUVP 80409 has one stapes preserved, lying behind the skull (Fig. 4).

Lower jaw.—Skulls of *Eoscopus* usually are preserved with the lower jaw. In spite of the number of jaws in the collection, the only adequate examples for description are the acid-prepared KUVP 80408 and 80409.

The symphyseal region of both mandibles is entirely visible. The expected fang-and-pit pairs at the anterior ends of the bones are present. At the symphysis, the dentaries enlarge to double the contact area, resulting in a projection into the angle of the jaw. This strengthening must exist because the jaw is slender at the symphysis. The inner end of each dentary is hollowed ventromedially by the meckelian sulcus. The anterior splenial follows the sulcus and most likely participated in the symphysis, although all four of the preserved splenials are broken before reaching this point (Fig. 5).

The posterior ends of the jaw are not as well preserved as the anterior ends and nothing can be said about the articulation or the adductor fossa. A single meckelian fenestra can be seen on the right side of KUVP 80408. It is a small, oval opening between the prearticular, angular, and postsplenial.

The exterior surface of the left jaw is visible, and the angular bone is more heavily sculptured than the dentary. This is also true of *Dissorophus* and *Broiliellus* (DeMar, 1968). The angular in *Eoscopus* lacks the ventral keel present in *Dissorophus,* however. Sharp, recurved denticles cover the dorsomedial part of the jaw and extend from the region of the symphysis to the presumed position of the adductor fossa. The coronoid bones that bear the denticles cannot be described because of their position. The contact between the two splenials is well preserved on KUVP 80409.

Vertebrae.—Six specimens have complete series of presacral vertebrae, lying in line and with the arches more or less in position. These are HQ 551, 598–599, and 720, and KUVP 47270 and 80412. Despite their completeness, none of these is unobscured in all parts of its column, and only KUVP 47270 can provide a vertebral count. Most likely, KUVP 47270 has 24 presacral vertebrae (Fig. 6). It is impossible to count the postsacral vertebrae of either KUVP 80412 or HQ 551, but there must have been at least 50. Caudal vertebrae diminish rapidly in size posterior to the ribs.

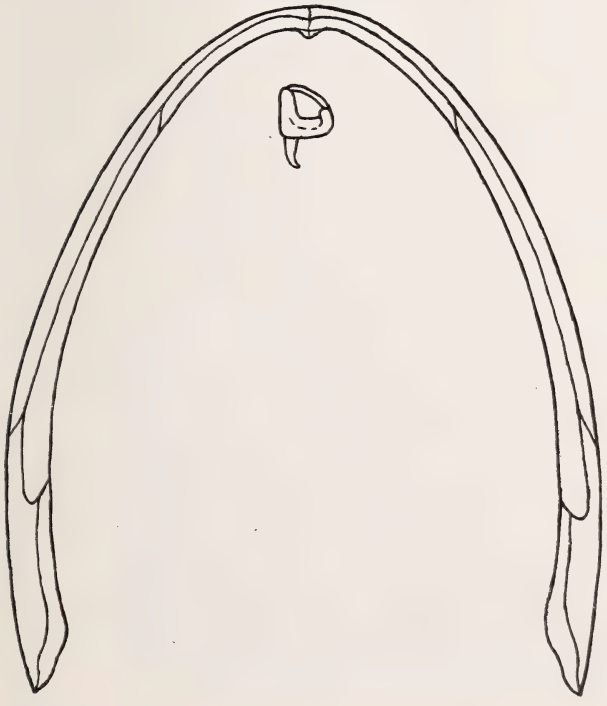

Fig. 5. *Eoscopus lockardi,* gen. et sp. nov. Reconstruction of the lower jaw in ventral view, × 2. Inset, an enlarged view of the anterior end of a half jaw.

The presacral neural arches are best observed on the acid-prepared specimen KUVP 47270 and on HQ 250F. In lateral view, the neural arch of each middorsal vertebra shows a long posterior sweep behind the pedicel. The neural spine surmounts this unsupported posterior region. The shapes of the neural spines vary regionally; on the first seven arches, the spines are square in profile, whereas for a typical middorsal arch each spine is a smoothly arched hump (Fig. 7). The anterior zygapophyses face anteriorly by 30–40°. The arches are not coossified in the midline, and the right and left halves are often shifted relative to each other.

Internal views of the neural arches are available on KUVP 47270 and 49491. The vertebrae are exposed in ventral view, and the inside of the slightly spread arches are visible between intercentra. On the inner surface of each neural arch pedicel, *Eoscopus* bears a pit, which must have lain opposite the spinal cord in life. On KUVP 47270, a large specimen, the pits shown on arches 10–15 are deep and open, except on the 11th arch, in which the opening is half covered by bone so that it faces posteriorly. KUVP 49491, a much smaller specimen, has shallower pits surrounded by thin rims restricting the opening.

The arch pedicels rest on triangular parachordal processes, the apices of which lie halfway down the sides of the vertebral centra (HQ 250F). The posterior edge of each triangle is noticeably longer than the anterior one. Elongated transverse processes, corresponding to the joined rib heads, incline anteroventrally, parallel to the posterior edges. The articular surfaces face posteroventrally and laterally. They were finished in cartilage rather than bone, like the zygapophyses. Preservation of transverse processes depends greatly on the extent of ossification at death. In KUVP 47270, the upper borders of the rib facets appear to be the lower edges of the parachordal processes, while on KUVP 80408 transverse processes are not visible at all.

Although many specimens have vertebrae, few have centra well-enough preserved to be readily interpretable. The intercentra are much more commonly observed than

Fig. 6. *Eoscopus lockardi*, gen. et sp. nov. Most of the vertebral column, KUVP 47270, ×2.

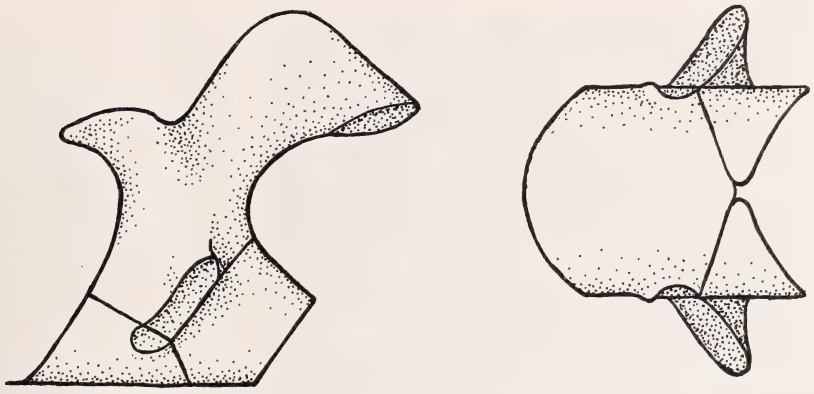

Fig. 7. *Eoscopus lockardi*, gen. et. sp. nov. Reconstruction of a middorsal vertebra in lateral and ventral views. Based on HQ 250F, × 7.

pleurocentra, which are less ossified, especially in younger individuals. The central elements are well displayed on HQ 250F, where a short segment of the middorsal column is preserved with all the elements well ossified and lying almost in their original positions.

The height of the intercentra is not great when compared to their other dimensions. Their posterior edges are angled where they lose contact with the pleurocentra and contact the neural arches. On a complete, well-ossified specimen, it is possible to distinguish the posterior face by the presence of this angle. None of the intercentra in the collection bears visible rib facets, with the single exception of one on HQ 250F. In this case, the facet is just above the posterior corner.

The well-ossified dorsal pleurocentra of HQ 250F are large in lateral view. Their long dorsal contact may have been co-ossified above the notochord. Like the intercentra, the pleurocentra have corners at the level of the ventral apices of the parachordal processes. However, the pleurocentra have corners on the anterior edges rather than the posterior. Ventrally, the pointed tips of the pleurocentra approach each other closely, usually preventing contact between adjacent intercentra. The centra of *Eoscopus* resemble those of *Micropholis* in this respect (Broili and Schröder, 1937). Specimen KUVP 49491, which has been partially uncovered by acid treatment, revealed a damaged presacral column in ventral view, where the pleurocentra are clearly visible (Fig. 8).

On KUVP 49491, pleurocentra are well preserved in the round. These do not conform entirely with the pleurocentra described from HQ 250F; they lack the dorsal development that allows a long contact above the notochord. The pleurocentra are roughly rhombic with the anterior corner slightly ventral to the middle of their height. The posterior, rounded corner is high and the pleurocentra may have had slight contact above the notochord. The difference between these pleurocentra and those of HQ 250F may reasonably be ascribed to ontologic variation, because KUVP 49491 is a smaller individual.

Pleurocentra are observable on KUVP 80408 also. The vertebrae of this specimen are laterally compressed, and only the pointed dorsal halves of the pleurocentra of one side are preserved as impressions. There is less dorsal development than in KUVP 49491. There is no dorsal, posterior corner, and the pleurocentra may not have touched above the notochord. The position of these vertebrae is farther anterior in the column, and this may influence the size and shape of pleurocentra.

KUVP 49491 affords a view of the inner or notochordal surfaces of the central elements. Andrews and Westall (1970:272) published a description of this part of the osteolepiform fish *Eusthenopteron* that also applies to KUVP 49491. The inner surfaces of the central elements are made of unfinished bone of an unusually close texture, and are covered with irregular vertical ridging.

KUVP 80409 and 47270 provide lateral views of the atlantal neural arch. This arch is two thirds as

Fig. 8. *Eoscopus lockardi*, gen. et sp. nov. Femur, pelvis and lumbar vertebrae, KUVP 49491, × 2.5.

long anteroposteriorly as those following it, and it exists as two half-arches, unfused to any central element. Transverse processes are absent. The anterior zygapophyses face anteriorly at about a 45° angle. The neural spine rises on a slope, so that its posterior corner lies just above the hindmost point of the posterior zygapophyses.

The axis is nowhere well preserved, but what can be seen of it on KUVP 47270 and other specimens indicates that it is similar to the vertebrae posterior to it, except that the neural spine is anteroposteriorly enlarged. It bears transverse processes and ribs, as can be verified from KUVP 80408.

The sacral arch can be seen on KUVP 47270, with an associated sacral rib (Fig. 6). In isolation, it can be readily identified by its enlarged transverse processes and anterior zygapophyses. The arch immediately preceding the sacral arch is correspondingly marked by enlarged posterior zygapophyses. The pedicels of the sacral arch are somewhat larger than those of other vertebrae, and show heavy vertical grooving that fans onto the anterior zygapophyses and the base of the neural spine. The neural spine is not preserved but it seems probable that it was higher and more square than those of its neighbors.

Eight rib-bearing vertebrae follow the sacral. The last of these bears the first haemal arch, as in *Eryops* (Moulton, 1974). KUVP 80412 shows an array of haemal arches in lateral view. Unfortunately, the central elements are unossified. The haemal spines are robust and diminish in length posteriorly in a regular fashion. Four vertebrae with haemal arches terminate the series preserved on KUVP 47270. The haemal canal occupies about half the height of the whole structure (Fig. 9). The legs on either side of the canal are laterally compressed and are narrow when viewed from the anterior or posterior. The spine itself is round and heavy, and socketed at the end, indicating that it was continued by a cartilaginous segment.

The neural arches do not have lengthened neural spines in the tail. The five anteriormost caudal arches have spines with a low square profile. More posteriorly, the anterior corner disappears and the spines slope toward the highest point at the rear of each arch. The dorsal portion of each caudal neural arch is smaller relative to the parachordal parts than is true of the dorsal vertebrae, and the caudal neural arches are not lengthened behind the pedicels.

Ribs.—All the ribs of *Eoscopus* are double-headed, with the heads conjoined with bone. They often show two articulating faces on the heads, meeting at a projecting apex at about 140°. The distal segments of the ribs are dorsoventrally flattened and have square ends.

Regionalism is evident (Fig. 10). The first pair of ribs is borne by the axis. Length increases to the fourth pair, then diminishes through the eighth pair. Behind the shoulder ribs, a series of similar dorsal ribs extends to the sacrum; thus, there is no pectoral region in the rib series of *Eoscopus*. There is a single

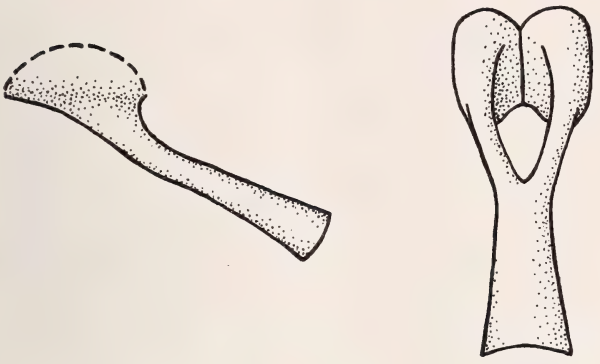

Fig. 9. *Eoscopus lockardi*, gen. et sp. nov. Reconstruction of a haemal arch in lateral and ventral views, based on KUVP 47270, × 6.

sacral pair, and eight pairs of caudal ribs follow the sacrum.

A complete series of shoulder ribs is displayed on KUVP 80411 and 80412. The anterior five pairs are preserved on one side of KUVP 80408, and a few lie near the disarticulated anterior vertebrae on HQ 122B. The shoulder ribs curve gently; the longest of them is about half again as long as the ribs following. They are narrowest about one third of their length from the proximal end. The ribs vary regionally, in that the sixth, seventh, and eighth pairs are shorter than the four preceding ones (Table 3). The fourth pair, or the third and fourth pairs are the longest. The larger ribs sometimes are visibly angled where the shaft rotates to the plane of the distal end. On KUVP 80412, the five anterior pairs are markedly more robust than the three following, and the second pair has very wide distal ends. The third rib pair has the second largest distal ends on this specimen.

The dorsal ribs are all about equal in size. They are narrowest just distal to their heads, which are shaped like isosceles triangles. From their narrowest diameter, the dorsal ribs expand evenly to their square distal ends, which are narrower than the joined heads.

Examples of the massive sacral rib are available on KUVP 47270, and HQ 250H, and 252. The sacral rib has a large oval head, a thick waist located at a third of its length, and a wide-bladed distal portion. That of KUVP 47270, the most complete available, is about 13 mm long, 5 mm wide at the head, and 9 mm at the distal end. The sacral arch bearing it is about 7 mm long. The head and the flat blade are only slightly turned with respect to each other. Grooving similar to that on the arch pedicel runs longitudinally on the waist of the rib, spreading onto the blade. The rib is slightly arched from end to end. The sacral rib of HQ 250H differs from the others is that it is curved from edge to edge (convex dorsally) also.

A series of caudal ribs is visible on KUVP 47270, and three pairs are partly exposed on HQ 250H. The two anterior pairs are straight, strong, and square-ended; they are nearly as long as the sacral rib. The remaining six pairs curve posteriorly. Of these, the middle four pairs are thick, square-ended, and extend two vertebrae posteriorly. Their two heads are delimited by an indentation in the bone bridging them. The two last pairs of ribs are short and pointed, and their heads cannot be distinguished.

Pectoral girdle.—Four specimens possess parts of the pectoral girdle. HQ 250E has most of a scapular blade, possibly part of another scapulo-coracoid, and most of a clavicle. HQ 551 has a pair of scapulocoracoids, a pair of clavicles, and a bone that may be the interclavicle. The third specimen, HQ 641, bears a scapulocoracoid with the scapular part preserved as an impression. KUVP 80411 has the interclavicle and possibly both clavicles.

The scapula of HQ 250E is short and broad, and has superficial sculpturing consisting of fine vertical grooves, each with a

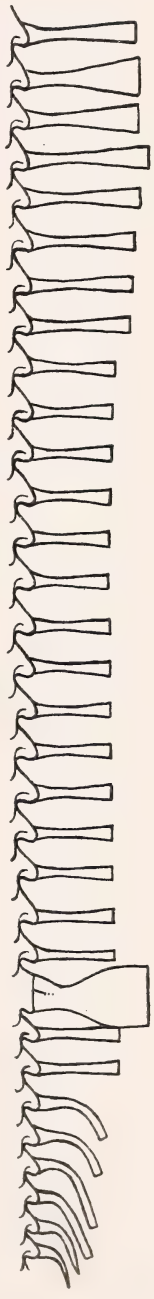

Fig. 10. *Eoscopus lockardi*, gen. et sp. nov. Reconstruction of the rib series, based on KUVP 80412A and KUVP 47270. × 2.

Table 3. Measurements of anterior ribs of *Eoscopus lockardi* in cm.

Rib pair	KUVP 80408 left	KUVP 80411 left	KUVP 80411 right	KUVP 80412 left	KUVP 80412 right
1st	0.70	—	0.67	—	0.70
2nd	0.80	—	0.72	0.73	0.74
3rd	0.88	—	0.80	0.73	0.74
4th	0.88	—	0.83	0.77	0.78
5th	0.73	0.77	0.80	0.74	0.72
6th	—	0.72	0.72	0.68	0.64
7th	—	0.72	0.70	0.66	—
8th	—	0.69	0.70	0.69	—
9th	—	0.50	0.50	0.55	—
10th	—	0.54	—	—	—
11th	—	0.49	0.47	—	—

small pit or foramen at its ventral end. HQ 551A is a much smaller animal, and the scapulocoracoids are quite different in shape. They are waisted and symmetrical on either side, like bow ties. The best scapulocoracoid is that of HQ 641 (Fig. 11). The bone is crescentic, but the lower arm is truncated rather than pointed. At the transition from the scapular portion to the coracoid portion of the bone, it bends at an angle slightly more than 90 degrees. Because the edge of the angle is not parallel to a line bisecting the crescent, but rises anteriorly, the coracoid portion has more area than the scapular. A deep impression in the stone preserves clearly the thick, robust area of the supraglenoid buttress. The bone is much thickened below and behind the buttress, until near the posterodorsal corner. Although the coracoidal portion is preserved as bone, this lateral area was removed in order to demonstrate its thickness. The glenoid fossa is not preserved, nor are there any traces of foramina; however, a deep pit is present on the inner surface just below the glenoid area. Evidence for its existence was a smooth-topped stone projection, uncovered while removing the lateral part of the coracoidal plate. The projection has been accidently removed. The pit may be the subscapular fossa, which ought to be present in this position. However, the pit is narrow and no foramina appear to open into it.

The split interclavicle of KUVP 80411 (Fig. 12) presents the medial side of its exterior half. Its silhouette is approximately hexagonal, with the two anterolateral faces concave. The exterior anterior half bears grooves, which radiate anteriorly from the center of the bone. Thirteen of them can be counted as matrix stripes. Originally the anterior border of

Fig. 11. *Eoscopus lockardi*, gen. et sp. nov. the scapulocoracoid and humerus of HQ 641, × 2.5.

the interclavicle may have been scalloped or dentate. The exterior surface is ornamented where it is not grooved or overlapped by the clavicles, as can be seen from the irregular appearance of the posteromedial portion of the bone.

The clavicle of *Eoscopus* (Fig. 12) is long-stemmed and lacks surface ornament on its ventral expanded portion. The dorsal portion is well preserved on HQ 250E and is as tall as the scapula lying slightly posterior to it. It curves smoothly where it rounds the anterior edge of the scapula (and presumably the ventral end of a cleithrum). A low keel arises near the ventral end of the stem, becoming most prominent just below the angle and descending toward the point of the leaf-shaped ventral plate. The angle between the stem and the plate is about 135°; in addition, the plate is rotated clockwise with respect to the slanting stem, so that it lay more or less horizontally in the body. An enigmatic feature of the clavicle of *Eoscopus* is the flat triangular process projecting from the anterior border of the stem, at about a third of its length. This process is visible on both the clavicles of HQ 551A, and is relatively larger in this smaller individual. A possibly homologous anterior process was described for the clavicle of *Dissorophus multicinctus* by DeMar (1968). The cleithrum described for *Branchiosaurus* by Boy (1978) much resembles a rotated *Eoscopus* clavicle, but note that in *Branchiosaurus* the triangular projection is on the opposite (articular) side of the stem.

Pelvic girdle.—There are eight pelves preserved in the collection, the best of which is HQ 123A and B. All of the bone was removed from the part and counterpart of this specimen, and silastic casts made, which display the internal and exterior surfaces of most of a whole pelvis (Fig. 13). In the next best specimen, HQ 250H, there is an impression of the interior surface of a half-pelvis. Both of these pelves have the pubes, which were unossified in smaller specimens (KUVP 49491, 80411, and 80412, and HQ 127, 247, 252, and 551A). No puboischial suture line is visible on the two with complete ventral plates.

Both acetabula can be seen on the cast of HQ 123B, and the upper part of another is exposed on KUVP 49491. The articulation surface is distinct, and has the expected posterodorsal indentation. Another, smaller scallop is present anterodorsally, such that the surface has an upper lobe. The acetabulum has projecting rims dorsally and ventrally, but there is no supra-acetabular buttress.

The iliac blade is straplike with a squared end, and curves posteriorly. Its anterior edge bears a

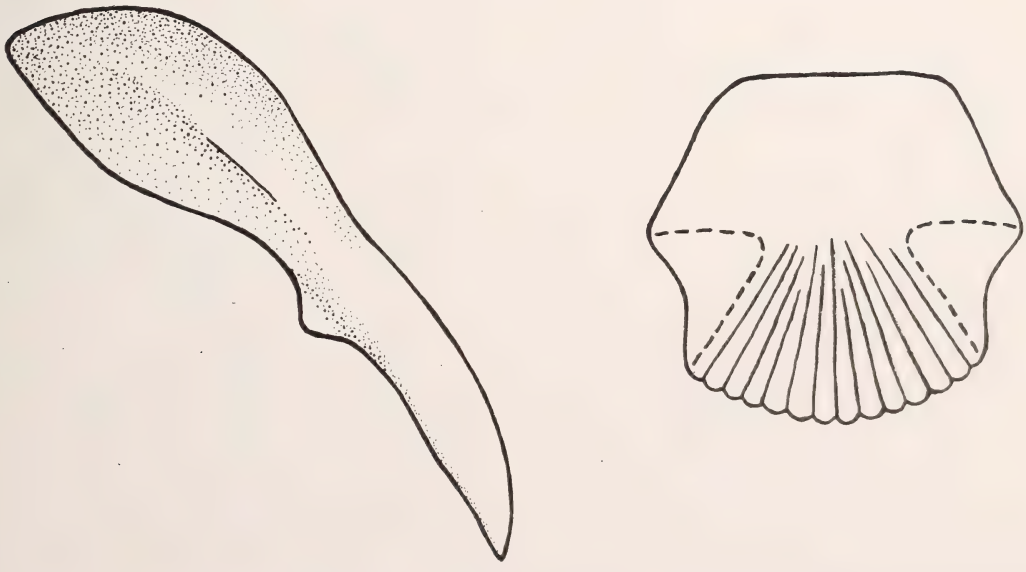

Fig. 12. *Eoscopus lockardi,* gen. et sp. nov. Reconstructions of the interclavicle and clavicle, × 5. Left: the interclavicle, based on KUVP 80411. Right: the clavicle, based on HQ 250E.

prominent hump, such that the ilium is almost two-pronged in silhouette. At the hump, the dorsal edge of the iliac blade bends and then runs straight posteriorly. The ventral, more robust edge curves more gradually. This feature of the ilium is well shown on the acid-prepared specimen HQ 252. The internal surface of the blade is faintly undulated, marking the sacral attachment. The cast of HQ 123 bears an additional deep groove through the dorsal edge of the iliac blade, running obliquely from the interior to the exterior. The groove pierces the crest immediately posterior to the bend in the iliac blade. The groove is continued by three ripples in the internal surface.

The suture line between the ilium and the ischium is marked on the internal surface of the pelvis by a slight ridge, accompanied by faint grooving perpendicular to it. On the external edge of the puboischiadic plate, a hump opposite the acetabulum marks where the bones meet. The suture line between the ilium and the pubis is not well marked; the ridge and the grooving diminish and disappear as they pass anteriorly.

The midline joint is best observed on HQ 123A, in which the contact is exposed. The halves of the puboischiadic plate originally met at an angle slightly greater than a right angle. The union between the right and left halves was deep and indicated by a ridge on the interior midline along the anterior two thirds of the plates. Posteriorly, the contact becomes a peg-and-socket arrangement. The right plate bears a rounded projection, which originally fitted into a matching indentation on the left plate, at the posteriormost point of the midline contact. The areas immediately anterior and posterior to the "peg" also interlock slightly. It is possible that a somewhat similar arrangement is present in the pelvis of *Ecolsonia;* Figure 12B in Berman, et al., (1985) is suggestive.

On HQ 123, the pubes are sharply everted or downturned along their anterior edges. On the ventral half (HQ 123B) this eversion is apparent as a ridge running between the acetabula, starting just posterior to the anterior corner on one side and passing in a slight arc across to the other acetabulum. In the interior view of the pelvis the pubes meet at an angle anteriorly, but this is not reflected in the edge of the deflected portion. The everted anterior portion of the pubis must be the area of origin of the puboischiofemoralis internus muscle in *Eoscopus.*

The cast of HQ 123B, showing the external side of the pelvis, has two large, round obturator foramina in the expected position. They are not visible on HQ 123A in a position opposite that of the outer

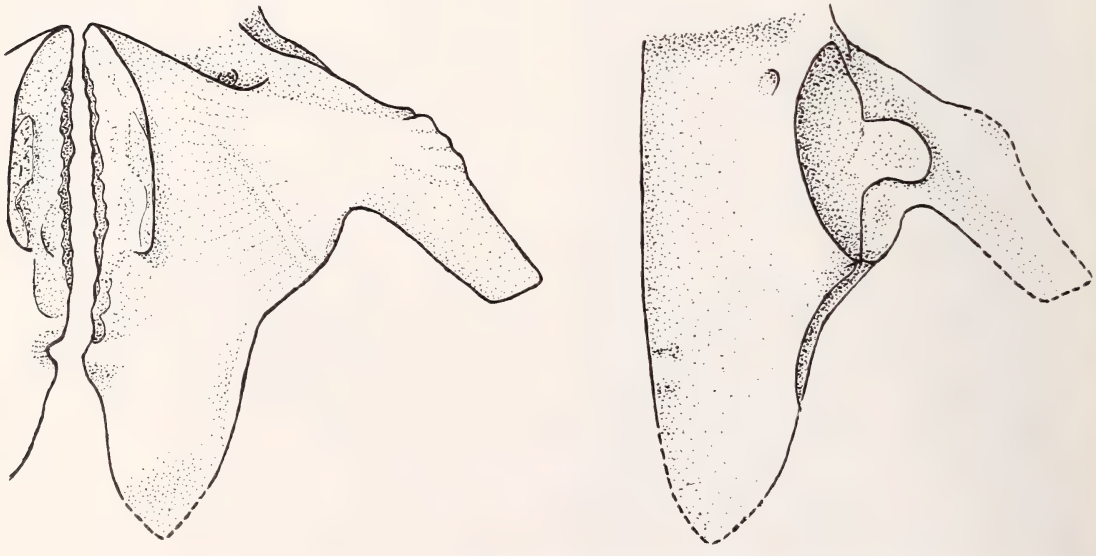

Fig. 13. *Eoscopus lockardi,* gen. et sp. nov. The pelvic girdle, from casts of HQ 123A and B, × 3. Left: the right internal surface. Right: the left external surface.

openings. Instead, two large foramina are visible on the downturned, anterior borders of the pubes. Apparently the canals run anterodorsally to open anteriorly. The pubes of *Eoscopus* are similar to those described for *Eryops* (Case, 1911), considering their difference in width.

Forelimb.—The humerus is moderately expanded at its ends and has a definite, if short, shaft with a round cross-section. Good examples of the humerus can be seen on HQ 250H (Fig. 14) and 641 (Fig. 11). Poor ones are present on HQ 551A.

The plane of the distal end of the humerus is rotated about 45° with respect to the plane of the proximal end of HQ 250H. There seems to be less rotation in the humerus of HQ 641, but this may be the result of flattening. The ends of both bones are smoothly rounded without processes or condyles. A deltopectoral crest projects from the anterior edge of the humeral head at right angles to the axis of the bone. This feature is a little more prominent on the smaller humerus (HQ 641) than the larger (HQ 250H). The bone is otherwise featureless except for fine longitudinal grooves on the surface of the head.

The distal portion of the forelimb is present on HQ 250H and 551A. The ulna bears an olecranon on the proximal end of HQ 250H; this is uncertain in the case of HQ 551A. The radius and ulna are equally thick and long if the olecranon is not considered. The radius and ulna bow slightly toward each other as they lie on HQ 250H. A keel runs down the posterior face of the ulna, from the proximal end of the olecranon to the distal end.

Nine wrist bones are present on casts made from HQ 250G and H. The wrists and ankles are unossified on HQ 551A. The nine bones probably do not make up the complete carpus, because Olson (1941) found eleven in the carpus of *Acheloma cumminsi* (as *Trematops milleri*). The element lying with the first metacarpal most likely is the first distal carpal, whereas the small nubbin between the last two metacarpals may be the fourth. The three bones just distal to the radius may be the ulnare, fourth centrale, and radiale, with the small intermedium considered missing. The other four carpals are interpreted as distals and centralia, with one of their number missing.

The four metacarpals can be observed on both

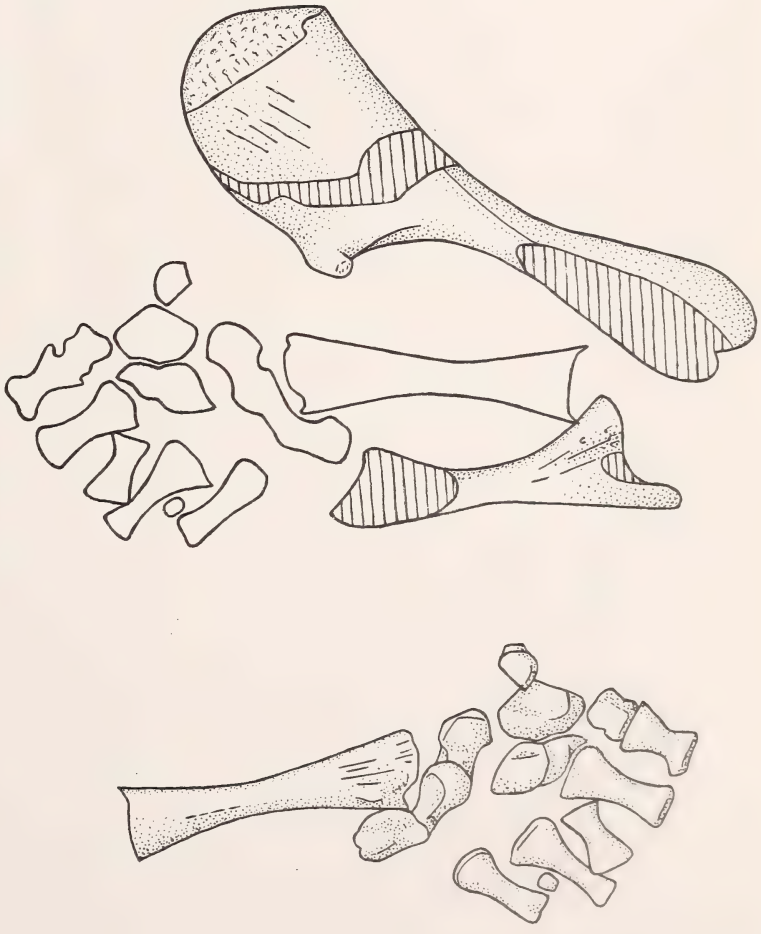

Fig. 14. *Eoscopus lockardi*, gen. et sp. nov. The forelimb, from HQ 250G and H, × 3. Above: humerus, ulna and position of natural molds. Below: radius, carpals, and metacarpals, from casts.

HQ 250G and H and 551A. The first metacarpal is the thickest and is about two thirds as long as the others. Metacarpals two through four become progressively more slender. They are straight, except for the fourth, which bends slightly towards the third. The third metacarpal has a smaller distal end than the others. All the metacarpals are short.

On HQ 250, only one phalanx is present, and on HQ 551A, both front feet are superimposed. Thus it is not possible to count the phalanges, but *Eoscopus* appears to have a rather blunt forefoot, with short digits. A terminal phalanx is unobscured on HQ 551A. It narrows abruptly from its articulation, as if to form a claw, but instead ends with a slight bulb.

Hindlimb.—Good examples of the femur are with specimens KUVP 49491, and HQ 123A and B, 250H and I, 252, and 431. Three specimens have been prepared with acetic acid and the other two have had the damaged bones removed from the matrix and silastic casts made of the spaces where they lay to allow observations of their intact sides. Perhaps the best femur is that of the casts of the part and counterpart of HQ 123, which show both sides of the bone (Fig. 15). Hindlimbs exist on specimens HQ 127, 253, and 551, but these are not well preserved.

The proximal end of the femur, viewed end-on, has approximately the shape of a curved teardrop, with the tail at the posterior side of the head. Apparently there are no distinctive features of the upper, convex surface of the femoral head; the rugosities on the femoral cast of HQ 250I are artifacts of preparation and the groove on the cast of HQ 123B is absent from other specimens. There is a prominent internal trochanter distal to the end of the femoral head, projecting at almost right angles to the plane of the head. In well-ossified specimens, such as HQ 123 and 250, the internal trochanter is stepped below the proximal end and separated by a notch. This morphology was described for *Caerorhachis* (Holmes and Carroll, 1977) and *Doleserpeton* (as *Cardiocephalus* in Gregory et al., 1956; *fide* Bolt, 1969).

The adductor flange continues the projection of the trochanter distally along the shaft of the bone. There is no posterior ridge and no fourth trochanter. On the two larger femoral specimens, the intertrochanteric fossa extends for about two fifths of the length of the bone. The adductor flange crosses the long axis of the bone distal to the intertrochanteric fossa, in passing from the internal trochanter to a terminus slightly closer to the posterior condyle. The flange diminishes in height distally, and finally blends into the shaft at the apex of the triangular popliteal concavity. On the dorsal side of the distal end, the intercondylar fossa extends about a fourth of the length of the bone. In end view, the posterior condyle is square and the anterior one more rounded, except for a projection marking the anterior side of the popliteal space. The distal end of the femur is straight on the shaft, or nearly so, and *Eoscopus* was probably able to completely extend its leg.

Good specimens of the tibia and fibula exist on HQ 123A and B, 252, and 431. Both bones have widely expanded ends, except for the distal end of the tibia, which is more modestly enlarged with a flat oval cross-section. As is typical in lower tetrapods, the tibia and fibula bow toward each other and the fibula is shorter than the tibia in most specimens. The fibula is nine tenths the length of the tibia in three measured specimens; however, in one case (HQ 123A and B) they are the same length. On both bones, the distal end of the bone is rotated about 45° with respect to the proximal end. This feature supplies half the torsion necessary to point the pes anteriorad. The expanded ends of the bones leave room for each other by lying at right angles; that is, the proximal end of the tibia is extended anteroposteriorly and that of the fibula mediolaterally, whereas the distal ends have the opposite relation.

The proximal end of the tibia is bilobed in end view, with the posterior lobe smoothly rounded and the anterior lobe sharply angulated by a prominent cnemial crest. The crest extends distally along the proximal expansion of the bone, which is about a third of its length. Both inner and outer surfaces of the tibial head bear grooving radiating proximally.

An unexpected feature of the tibia is a second crest running down the posterior or internal side of the shaft. This is revealed on the acid-prepared specimen HQ 431. The crest arises from the distal part of the head, and disappears at the distal expansion of the bone. A posterior crest has been described for the tibia of *Cacops* (Williston, 1910), but it may not be homologous. The crest of *Cacops* begins at the proximal end toward one side and has a small hump at its midlength. Possibly these crests increase attachment area for the interosseus cruris. In modern salamanders this muscle holds the tibia and fibula

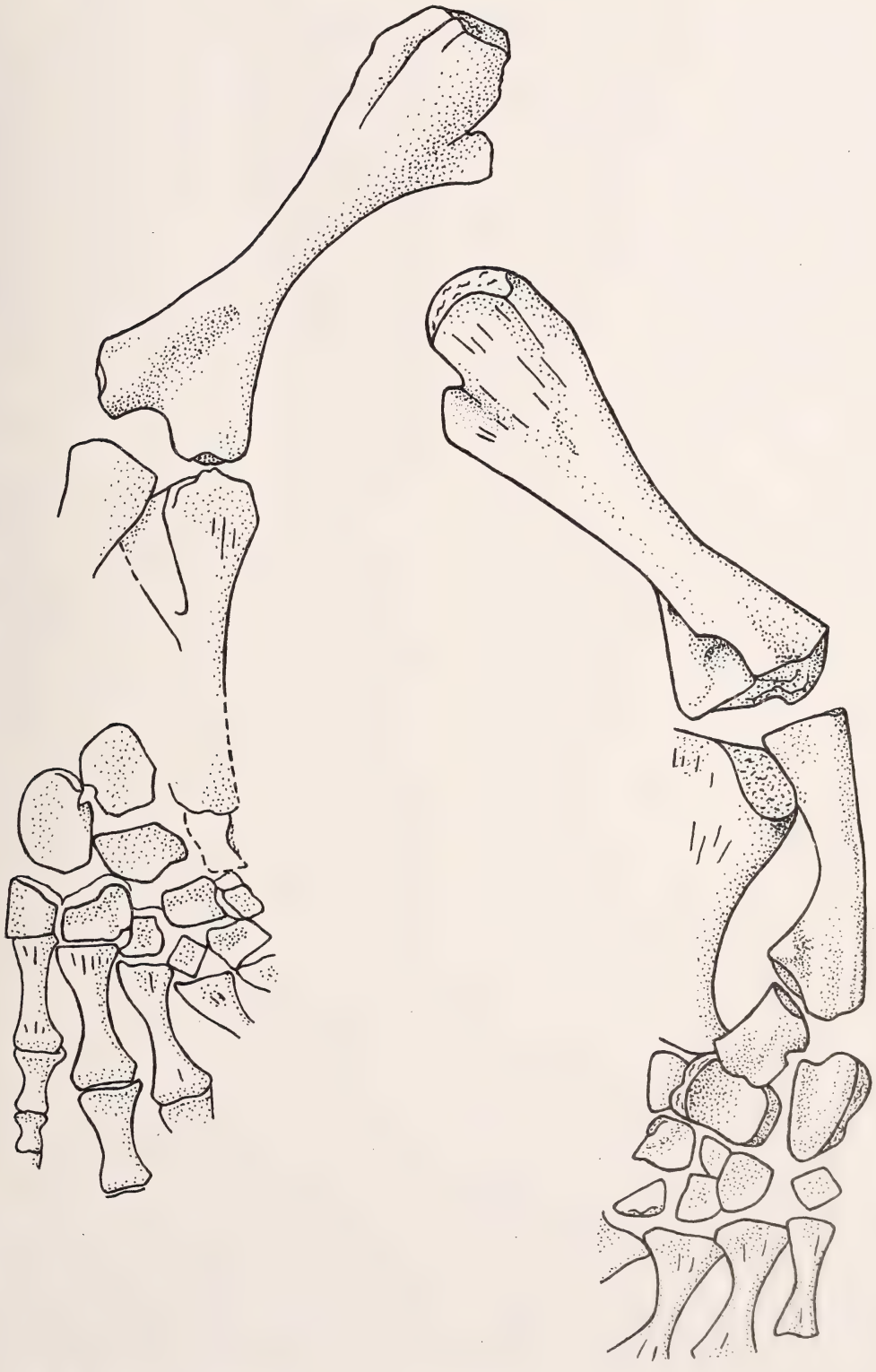

Fig. 15. *Eoscopus lockardi*, gen. et sp. nov. The hindlimb, from casts of HQ 123A and B, × 3. Left: anterior view, HQ 123B. Right: posterior view, HQ 123A.

together and assists in transfer of weight between them (Schaeffer, 1941).

The wide, flattened ends of the fibula have about equal areas in lateral view. It is not possible to observe them end-on in any specimen. The head of the fibula is flat or slightly convex in profile. Its distal end describes an S-curve, very noticeable in posterior view (HQ 123A), but more gentle in lateral or anterior view (HQ 252). This curved surface conforms to the articular surfaces on the intermedium and fibulare. The high medial corner of the distal end articulates with one side of the intermedium. A broad groove passes distally across the high corner (HQ 123A), possibly marking the passage of an artery connecting with the perforating artery which passes through the tarsus immediately distal to this point.

An ossified ankle with the bones in position is available in the collection. HQ 123A and B are part and counterpart bearing a pelvis with the right hind limb, lacking only part of the foot. The incomplete remains of the bone have been removed and silastic casts made for study from the impressions on the two sides. The posterior side of the tarsus is displayed on the cast of HQ 123A, and the anterior side on the cast of HQ 123B (Fig. 15). Part of HQ 250H also bears an ossified tarsus, which was prepared in the same way, but it is disarranged and incomplete. The tarsus was unossified in all other hindlimb specimens available.

The tarsus of *Eoscopus* resembles that of *Trematops,* as described by Schaeffer (1941). The name *Trematops* is now considered synonymous with *Acheloma* (Dilkes and Reisz, 1987) but it is convenient for Williston's and Schaeffer's name to be used in this section. The tarsus specimen was provided by E. C. Olson, then of the University of Chicago; it is not further identified.

Apparently the pretarsale present on the medial side of the ankle of *Trematops* is lacking in *Eoscopus*. This bone cannot be seen and there is no space for it to articulate with the distal end of the first centrale. On the whole however, it is appropriate to describe the tarsus of *Eoscopus* by comparing it with Schaeffer's account.

Gregory et al., (1923) described the carpus of *Eryops* as being originally arched, but flattened before fossilization; this also is the situation with the tarsus of HQ 123A and B. Its tarsal elements are a little hollowed on their ventral surfaces, indicating that the whole complex arched from side to side in life. Schaeffer (1941) did not mention such a feature for the tarsus of *Trematops,* perhaps because his specimen provides a view of the dorsal surface only. In that view it is not obvious that the tarsus of HQ 123 was originally arched; it seems only to have a rather broad foot.

Individual tarsal elements differ in the details of their outlines from one surface to the other. This was true for *Trematops* also, and it occasioned some of Schaeffer's corrections of Williston's (1909) original description. The type specimen affords a view of the plantar side rather than the dorsal. A good example of the resulting disagreements is the case of the intermedium.

The intermedium of *Eoscopus* and *Trematops* is a large bone between the tibia and the fibula, with a free proximal border that rises toward the high medial corner of the fibula. Its other borders contact the fibula, tibia, fibulare, and fourth centrale. Williston (1909) described the intermedium of *Trematops* without mentioning the tibia, but Schaeffer (1941) described and figured the bone with a large facet contacting the tibia, to which it was apparently ligamentously attached. The source of the error is revealed when both sides of a similar ankle are examined. The facet for attachment to the tibia is plain in anterior view (HQ 123B) but invisible in posterior view (HQ 123B). In both views, the intermedium has a definite rounded notch for the perforating artery in the border toward the fibulare. This must be a real difference between *Eoscopus* and *Trematops,* because neither Williston nor Schaeffer found it in the latter, although Williston thought that there was a gap between the intermedium and the fibulare.

In plantar view, the fibulare of *Eoscopus* is narrowest at its distal end rather than at its contact with the fibula, as reported by Schaeffer for the dorsal view in *Trematops*. Otherwise it conforms to the description of *Trematops,* with the same exception as that noted for the intermedium. The proximal end in posterior view has a marked step cut into the medial corner. When the fibula, fibulare, and intermedium were naturally aligned a gap existed between them at this corner, such that it continued

the space enclosed by the notch in the intermedium. On the dorsal side of the fibulare, a notch cut in the border matches that in the intermedium, such that the fibula does not participate in the rim of the passage on the dorsal side of the ankle.

The tibiale is like that of *Trematops,* except that it is much narrower. It articulates with the first, second, and fourth centralia.

The fourth centrale, the widest bone in the tarsus, most clearly shows the arch of the ankle in plantar view. An end view of this bone is possible on the cast of HQ 250H, in which the axis of the arch, the thickness of the bone, and its articular surfaces are evident. The fourth centrale resembles that of *Trematops.* Ventrally, the centrale is nearly rectangular, but larger on the tibial side, as shown in Williston; dorsally, its distal edge is V-shaped to provide two articulation surfaces, as described in Schaeffer. In *Eoscopus,* the fourth centrale contacts the tibia, as Schaeffer said it probably did in *Trematops.*

The other three centralia differ in details of shape from the descriptions of *Trematops.* The first centrale of *Eoscopus* is narrow and elongated to fill the space between the tibiale and the first tarsale. The second centrale is almost square in anterior view, but a little narrower mediolaterally in posterior view, to conform with the curve of the ankle. The third and smallest centrale deviates from a square only in that its proximal edge rises toward the fibular side in dorsal view, to follow the lower edge of the fourth centrale.

The shapes of the first two tarsalia of *Eoscopus* closely match those depicted for *Trematops* by Schaeffer. The first tarsale is a little squarer than in *Trematops.* It is slightly hollowed dorsally, proximodistally rather than from side to side. Its ventral surface is not preserved. The second tarsale is shorter than that depicted for *Trematops,* and the smallest of the series in *Eoscopus.*

The third tarsale of *Eoscopus* is more complex in shape. Its fibular edge is strongly concave, encroached upon by the fourth tarsale. Articulation with the second tarsale is straight, but the proximal border is concave to articulate with the second centrale. The proximal edge is distal to the third centrale and rises toward the tibial side. There is a slight central depression in the dorsal surface of the third tarsale, whereas the ventral surface is a little hollowed proximodistally.

Largest of the tarsalia is the fourth, as in *Trematops.* Unlike the relations described for *Trematops,* the fourth tarsale of *Eoscopus* does not contact the fifth metatarsal, or any metatarsal other than the fourth. Its greater width overlaps toward the third metatarsal, but the distal corner of the third tarsale prevents contact. The tibial side of the fourth tarsale is a long convex curve that borders the third tarsale, third centrale, and fourth centrale. Contact with the fifth tarsale is short and straight. The proximolateral corner of the fourth tarsale appears truncate, because the articulation with the fibulare is straight and diagonal, matching the inner of the two slanting faces on the distal end of the fibulare. The line of contact on the tarsale is everted, so that the edge is raised and the articular surface faces slightly dorsally (covered in life by the fibulare). Inspection of Schaeffer's Figure 1 shows that *Trematops'* fourth tarsale is also like this. When seen in plantar view, the lateral side is quite different: the distolateral corner of the tarsale is rounded and everted, and the portion near the fibulare is slightly cornered.

The fifth tarsale is narrow distally, to match the narrow-headed fifth metatarsal. It becomes wider proximally by enlarging laterally until it covers the remaining half of the fibulare. Its proximal face slants ventromedially, along with the lateral sloping facet of the distal end of the fibulare. The line of contact is everted on the fifth tarsale, as it is on the fourth. In plantar view, the fifth tarsale is not wider dorsally, everted, or hollowed.

Consideration of all the tarsalia leads one to believe that the shape of the tarsus of *Eoscopus* is more complex than a simple arch. A dorsal concavity must exist at each side of the more distal part of the ankle. This interpretation accounts for the dorsal hollowing of the first tarsale, and the everted proximal articular surfaces of the fourth and fifth tarsalia. The physical traces are considerably more marked laterally on the ankle because the long straight fibulare concentrates the curvature. The peculiarities of the plantar surfaces of the tarsalia are not readily explained.

The metatarsals are best observed on the silastic casts of HQ 123A and B, which display them in dorsal and ventral views. KUVP 80412 and HQ 252

provide another view of the first two metatarsals, not wholly preserved on HQ 123. On these specimens the first metatarsal is thickest and about two thirds the length of the others, the fourth metatarsal is the longest, and the fifth has smaller ends than the others. The metacarpals are 70% as long as the metatarsals, as can be verified by making measurements of HQ 250. As is typical of temnospondyls, the hindfeet of *Escopus* are longer than its forefeet. The heads of the metatarsals are marked on both sides with a few short longitudinal grooves of varying depth. As can be seen from either of the casts of HQ 123, the metatarsals are not quite straight, but are slightly skewed medially, as if the twist necessary to point the foot anteriorad could not be provided entirely by the ankle.

The phalangeal formula of the pes of *Eoscopus* is 2–2–3–4–3. This was determined by inspection of the acid-prepared specimen HQ 252 (Fig. 16). The same formula has been reported for *Micropholis* (Broili and Schröder, 1937) and for *Micromelerpeton* and *Branchiosaurus* (Boy, 1972). DeMar (1968) said that the formula for *Dissorophus* was 2–3–4–4–2, but his judgment may have been influenced by that given by Schaeffer for *Trematops*. The pes of *Dissorophus,* shown in DeMar's Figure 17, can be interpreted more plausibly as 2–2–3–4–3. The phalangeal formula of *Escopus* appears to be common among temnospondyls. As with the front toes, the terminal phalanges of the hind toes have slender, delicate ends. These are not clawlike, but are straight and knobbed rather than pointed. The terminal phalanges of *Branchiosaurus* cf. *B. petrolei* and *Micromelerpeton* are known to have slightly enlarged ends (Boy, 1972). This toe form may be widespread.

A reconstruction of the possible appearance of *Eoscopus* in life is presented in Figure 17.

Amphibamus Cope 1865

The coal-swamp amphibian genus *Amphibamus* is composed of three known species from three different Westphalian D localities (see Fig. 1). Specimens of *A. lyelli* (Wyman, 1858) from Linton, Ohio, and *A. grandiceps* Cope 1865 from Mazon Creek Illinois, were examined.

Amphibamus has been carefully described from detailed, articulated specimens. Wyman (1856) first published a preliminary note on this new "batrachian" found at Linton. Many authors have dealt with the genus *Amphibamus* subsequently, including Cope, Moodie, Romer, Steen, J. T. Gregory, Watson, Carroll, Bolt, and A. R. Milner. Modern descriptions are Watson (1940, *A. grandiceps*), Gregory (1950, *A. grandiceps*), Carroll (1964, *A. lyelli*), Bolt (1979, *A. grandiceps*), Milner (1982, *A. lyelli* and *A. grandiceps*) and Hook and Baird (1984, *A. lyelli*).

The two American species were studied from

Fig. 16. *Eoscopus lockardi,* gen. et sp. nov. The ilium and hindlimb, HQ 252, × 2.5.

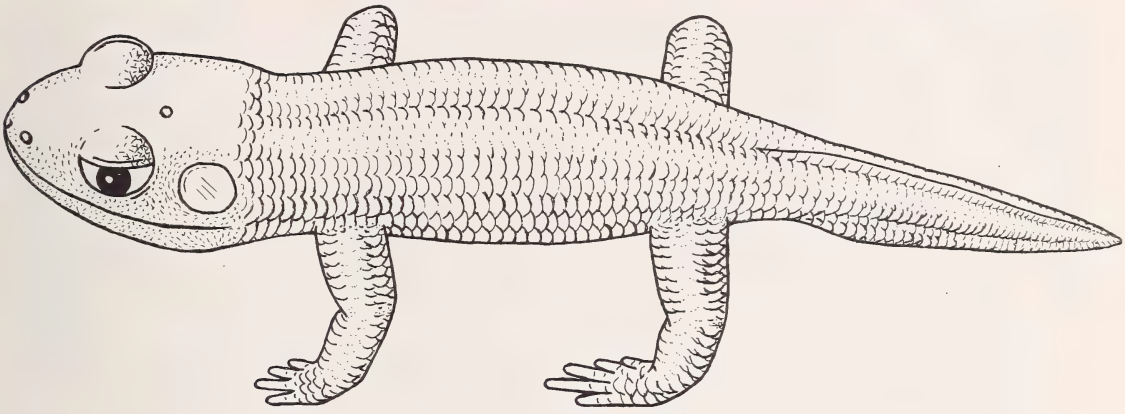

Fig. 17. *Eoscopus lockardi*, gen. et sp. nov. Reconstruction of appearance in life, based on HQ 551, × 0.875.

casts of natural molds. The holotype of *A. lyelli*, AMNH 6841, was made available as a plaster cast from the original coal block, showing the dorsal side of the animal. A latex cast of AMNH 2002 shows a lateral view of the posterior body and anterior tail of a larger individual. USNM 4461, a block of coal bearing an impression of the posterior trunk and a hind leg, was loaned for study.

The *A. grandiceps* specimens examined were three split Mazon Creek concretions, each showing most of a small individual in part and counterpart. They include YPM 794, the neotype (Fig. 18); YPM 795, the type of *Mazonerpeton;* and FMNH UC 2000, the type of *Miobatrachus*. The two Yale nodules were prepared for silastic casting by complete removal of their mineral infilling, exposing clear impressions.

Amphibamus specimens fall into size classes. The largest *A. grandiceps* (YPM 794) is about half the size of the smallest *A. lyelli* (AMNH 6841). All the nodule skeletons are of juveniles, although postmetamorphic (Carroll, 1964; Bolt, 1979). Despite their age difference and their great similarity, the specimens represent two species. Differentiating features include the number of teeth and the vertebral count (Carroll, 1964). Milner (1982) adds that *A. grandiceps* is smaller at metamorphosis, and that *A. lyelli* has a wider skull. His examination of a skull of a young *A. lyelli* made his distinctions possible.

Because *Amphibamus* was previously described, my original intent was to only point out characters of taxonomic importance. However, a number of interesting features, previously unknown, were discovered and the following description has therefore been broadened.

Skull.—The quadrate of *Amphibamus grandiceps* is much like that of *Doleserpeton* (Bolt, 1968). It is best viewed on the right side of the skull of FMNH UC 2000, where the lower jaw does not cover it (Fig. 19). The quadrate has a prominent dorsal process on its exposed medial corner, with a groove running up the posterior side and over the end (Bolt, 1979). This may be seen on the right side of YPM 794 also. The medial condyle is almost a mirror image of the dorsal process. In posterior view the quadrate is Y-shaped, with the arms facing medially, such that the articular surfaces face slightly outward. The quadratojugals of FMNH UC 2000 have a straight medial border with no sign of a posteromedial process on either side. YPM 794, however, shows this character on both sides. The posteromedial process in *A. grandiceps* covers part of the posterior side of the dorsal process of the quadrate, rather than embracing it as in *Eoscopus*. The quadratojugal does not contribute to the condylar surface, contra Watson (1940), but as observed by Bolt (1979).

A ventral prefrontal process is visible in the right orbit of AMNH 6841. Other features of the orbital area are not certain. A laterally exposed palatine may be present in the ventral rim. Another character diagnostic of the Dissorophoidea, the supratympanic flange, has never been observed on *Amphibamus*. The preservation of available specimens does

Fig. 18. *Amphibamus grandiceps* Cope. The neotype, YPM 794, × 4. A cast of the dorsal impression.

not permit inspection of the dorsal side of the otic notch.

Dorsal processes of the premaxillae have been depicted for the American species of *Amphibamus* (Milner, 1982:fig. 3). Examination of the cast of AMNH 6841 revealed narrow, sharp processes on either side of the muzzle. On the two *A. grandiceps* skulls examined, the dorsal parts of the premaxillae are not preserved, but the slots they once lapped into are observable on the nasal bones. On the left nasal of YPM 794 the dorsal process was leaf-shaped; on the right it had a medial point and a lateral lobe (Fig. 20). The left nasal of FMNH UC 2000 bears an impression similar to the left nasal of YPM 794 (the right is damaged). In FMNH UC 2000, the points of the dorsal processes were joined across the midline by thinner extensions of the premaxillae; possibly a juvenile characteristic. The form of the right premaxilla of YPM 794 has been described for *Platyhystrix* (Berman et al., 1981) and is depicted on

the right side of the muzzle of *Micropholis* (Broili and Schröder, 1937).

A nearly complete palate is visible on YPM 794 and FMNH UC 2000. All of the dermal bones are covered with denticles except the anteriormost part of the vomers. Denticulated skin is absent, unlike the palate of *A. lyelli* (Carroll, 1964). Tubercle-bearing platelets described by Steen (1931, as *Platyrhinops*) were also absent. This does not mean that such a covering was not originally present, or that it might not appear later in ontogeny.

The parasphenoidal denticle field continues anteriorly on the rostrum, borne on a raised strip that conforms to the width of the bone. The denticle field terminates in a point. *A. grandiceps* specimens have a groove for the internal carotid that crosses the base of each basipterygoid process, resulting in sharp borders on the denticle field. Each groove becomes a canal into the braincase, just posterior to the basal articulation. An indentation in each side of the denticle field marks the position of these canals.

YPM 794 bears a vomerine fang on the anterior end of one internal naris, but not on the other. A fang is present on each palatine and ectopterygoid. In contrast, FMNH UC 2000 has three small fangs or large denticles on the anteromedial rim of each internal naris. There are no palatine or ectopterygoid fangs. The row of palatine teeth described by Watson (1940) is present, as confirmed by Bolt (1979). There are additionally three more palatine teeth on the opposite side of the palate, close to the maxillary series. The palatine row included eight to ten teeth when intact, set along the contact with the maxilla. Change with age is the most plausible explanation for the difference between YPM 794 and FMNH UC 2000 (Bolt, 1979). Similar ontological change apparently occurs in *A. lyelli* as well (Milner, 1982).

Details of the basal articulation are well preserved on the two nodule skulls (Fig. 21). The internal process of the pterygoid and the basipterygoid region of the parasphenoid are seen in near-life positions on the left side of FMNH UC 2000. The processes appear to be transverse cylinders with an oblique contact. The palate of YPM 794 affords separated views of the pterygoid and basipterygoid processes. On the right, the free end of the basipterygoid process faces anteriorly and slightly laterally. It consists of a projecting rim enclosing an oval depression, indicating that it was unossified except for a bony cover. On the left, the internal process of the pterygoid is a narrow hollow cylinder laterally. The cylinder enlarges to match the wide oval of the opposite side of the joint. The concave internal surface of the internal process of the pterygoid faces posteriorly. The epipterygoids of *A. grandiceps* are ossified with large ventral ends. As in *Eoscopus,* they could not have participated directly in the basal articulation.

A reconstruction of the basal articulation of *A. lyelli*, shown in Carroll's Figure 22 (1964), resembles the morphology in *A. grandiceps*. The accompanying text stated that the relevant areas of the best available specimen were damaged and that the reconstruction was made using *Tersomius* from Archer City. *Tersomius* is depicted in Carroll's Figure 4. Milner (1982) presented the palate of juvenile *A. lyelli* with a conventional reconstruction of the articulation; i.e., a right-angle rather than oblique contact. Thus the configuration of the basal articulation of *A. lyelli* is still undescribed and unknown.

Vertebrae.—Carroll (1964) stated that AMNH 6841 has 25 presacral vertebrae and this has been verified. YPM 794, the neotype of *A. grandiceps,* has 20 presacrals. FMNH UC 2000 seems to have 20 presacrals, as Watson (1940) thought it might. For my count of FMNH UC 2000, I identified the sacral as the last vertebra with a wide pedicel (as did Watson), because I cannot discern sacral ribs on my cast.

In general, the neural arches of *Amphibamus* are as described by previous authors. The atlantal arch of *A. lyelli* resembles that of *Eoscopus,* except that *A. lyelli's* neural spine does not slant posteriorly as much and the arch is fused to a central element. The atlantal arch of *A. grandiceps* is visible in lateral view on the ventral cast of YPM 794, and is not fused to its centrum, possibly due to its youth. The large parachordal processes of *Amphibamus* are much like those of *Eoscopus*. The transverse processes parallel the posterior edges, which are longer than the anterior edges. Only the dorsal portions of the transverse processes are preserved on FMNH UC 2000 and they are as Watson (1940) described them.

The impressions of the nodule halves of YPM 794 were completely cleaned for this study. The

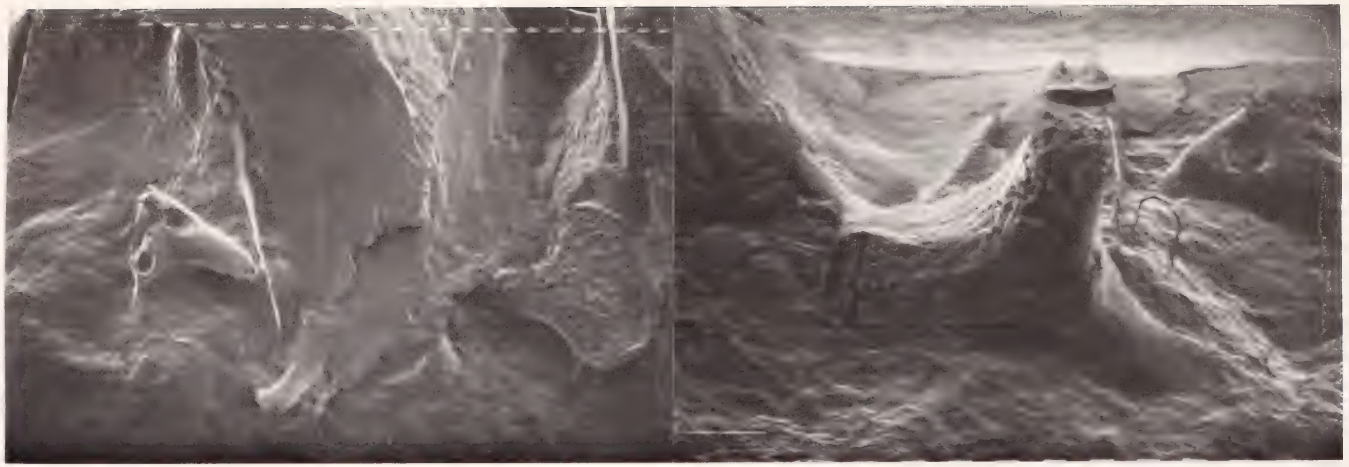

Fig. 19. *Amphibamus grandiceps* Cope. The quadrate in SEM photomicrographs of casts. Left: a posterior view of the right otic notch of YPM 794, × 20. Right: a posterior view of the right quadrate of FMNH UC 2000, dorsal process on the right, × 40.

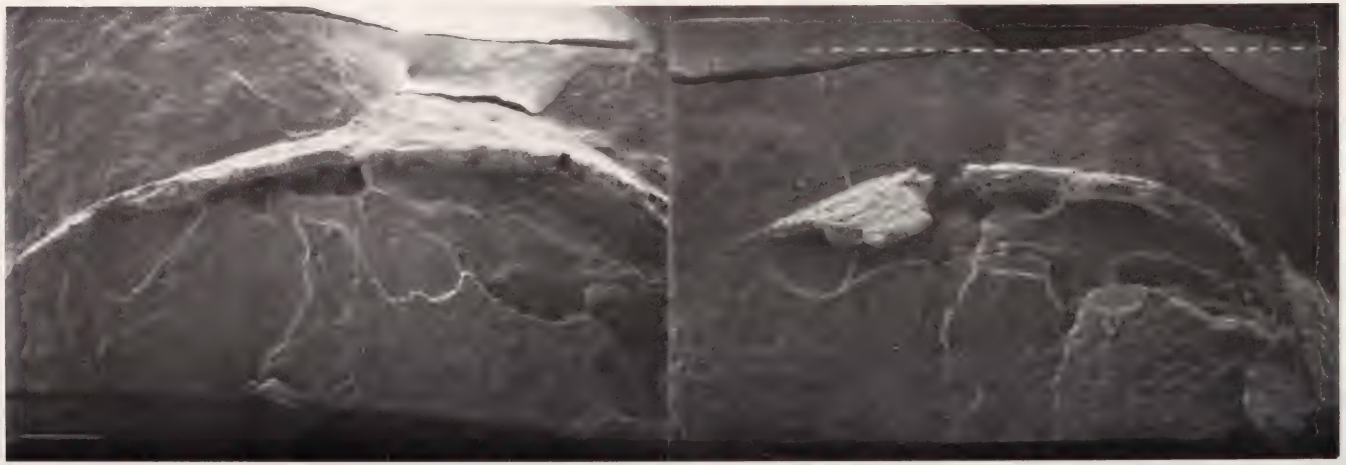

Fig. 20. *Amphibamus grandiceps* Cope. The impressions for the premaxillae on the nasals, ×15. SEM photomicrographs of casts. Left: YPM 794. Right: FMNH UC 2000.

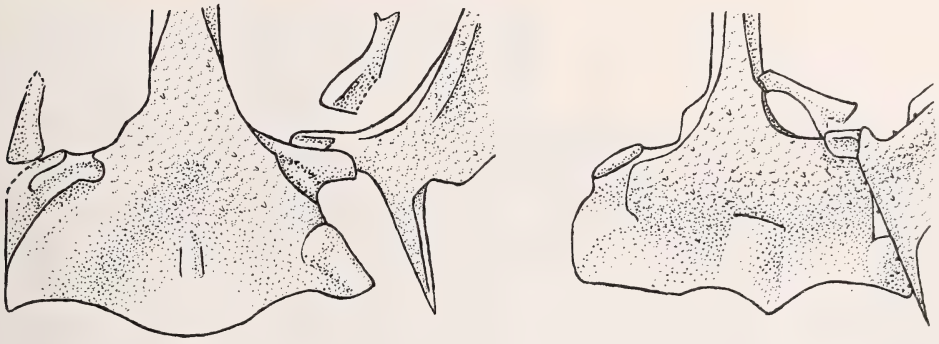

Fig. 21. *Amphibamus grandiceps* Cope. The posterior palate, from casts. Left: FMNH UC 2000, × 10. Right: YPM 794, × 7.5.

dorsal view of the vertebral column shows the chain of neural arches lying in order. The neural spines, if present, would extend into the nodule and cannot be seen. Many of the anterior zygapophyses can be inspected and their articular surfaces are unossified, as in *Eoscopus*.

The ventral nodule half of YPM 794 presents a view of the ventral sides of the neural arches. Impressions of the lower parts of the prezygapophyses identified this previously mysterious vertebral series. The portion of the arch that rests on the notochord possesses an anterior and posterior widening, delimited by a slight annular constriction. On the eighth and ninth arches the neural canal is visible. The neural canal has anterior and posterior chambers, separated by a definite ridge. These chambers are not opposite their counterparts on the parachordal portion. If these are traces of resegmentation (sensu Williams, 1959), the arches must have formed in separate parachordal and neural parts. The ridges of YPM 794 may be homologous with the vertical ridges described within the neural canals of *Doleserpeton* (Bolt, 1968).

The pleurocentra of *A. grandiceps* are clearly visible on YPM 795 (Fig. 22). In lateral view, the pleurocentra are the largest central elements and the pleurocentral pairs must have a long contact ventral to the notochord. Ventrally, the pleurocentra are nearly as large anteroposteriorly as the intercentra. Watson (1940) based his description on the near-ventral view available on FMNH UC 2000, where the central elements have been rotated around the notochord. In its original condition, the column of FMNH UC 2000 must have closely resembled that of YPM 795. This is clearest in the posterior dorsal and anterior caudal portions (Fig. 23; also Bolt, 1979:fig. 9). The element in the center of the photograph (Fig. 23) may be the inside of the opposite neural arch.

The pleurocentra of *A. lyelli* are well preserved in the posterior column of USNM 4461 (Fig. 24). This specimen was laterally compressed, causing the long pleurocentra to be flattened out onto a plane. Their bluntly-pointed ventral extensions project ventral to the column, and their shape is easily observed. These pleurocentra are clearly cornered anteriorly, as in *Eoscopus*. An unflattened, disarticulated pleurocentrum lies ventral to the vertebral column on AMNH 2002.

The dorsal intercentra are like those of *Eoscopus*. The well-preserved intercentra of USNM 4461 show a low projecting angle on either side of their posterior edges, where the intercentra change their contacts with the neural arches and the pleurocentra. Articular facets for the capitula of the ribs are lacking.

The pleurocentra in the tail of YPM 795 are similar to those illustrated in Gregory (1950). The dorsal portion of the caudal intercentra are broken off on the nodule-half bearing the dorsal side of the skull. The intercentra are reduced in comparison to the trunk vertebrae, and it is possible that they were partly cartilaginous (Fig. 23). The preserved tails of AMNH 2002 and FMNH UC 2000 bear large, well-ossified intercentra, in contrast to YPM 795.

The haemal arches of *Amphibamus* resemble those of *Eoscopus*. On FMNH UC 2000,their legs are anteroposteriorly expanded as they approach the

Fig. 22. *Amphibamus grandiceps* Cope. Dorsal vertebrae in lateral view, × 15. SEM photomicrographs of casts. Left: YPM 795. Right: FMNH UC 2000.

intercentra to which they are attached. The caudal intercentra of AMNH 2002 appear to be fused in the ventral midline. On YPM 795, the first haemal arch is probably borne on the fourth postsacral. This also appears to be the case in FMNH UC 2000.

Watson (1940) identified the very large, dominant central elements of the anterior tail of FMNH UC 2000 as pleurocentra, because of their rhombic shape. It is tempting to identify them as intercentra, because of the prominence of the the intercentra immediately posterior to them. Examination of the tail region of YPM 795 revealed large cylindrical elements. In this specimen, these elements are best identified as pleurocentra, because they are dominant posteriorly; furthermore, only pleurocentra extend the full height of the notochord. Restudy of FMNH UC 2000 shows that the large central elements are incomplete cylinders that are open dorsally and have a slight angulation to their anterior edges. Therefore, the large central elements in the anterior tail of FMNH UC 2000 probably are pleurocentra, as Watson thought.

Ribs.—*A. lyelli* has short ribs throughout the column. Three pairs of shoulder ribs begin on the third vertebra. Absence of axial ribs is related to the position of the occiput, which is considerably anterior to the jaw articulation. The shoulder ribs are thicker than those posterior to them, with double joined heads and expanded ends. Unlike the shoulder ribs of *Eoscopus*, they are not noticeably longer than the other ribs. Two pairs of transitional ribs follow (see Fig. 23 in Carroll, 1964). One shoulder rib and one transitional rib can be seen on YPM 794, so *A. grandiceps* probably was similar. Two shoulder ribs are preserved on YPM 795.

Typical mid-dorsal ribs are slender, slightly curved, and square-ended. They have two distinct heads joined by a web of bone (FMNH UC 2000). The flanges described by Carroll are visible only on the large specimen, USNM 4461 (Fig. 24). The square ends of the dorsal ribs indicate cartilaginous continuations in the living animal. An *Amphibamus* nodule from Mazon Creek (the Daniels specimen) had preserved rib extensions (Hay, 1900). The nodule is lost (Gregory, 1950), but figured in Moodie (1916). The apparently long ribs of the Daniels specimen previously caused confusion in the taxonomy of *Amphibamus*.

The tapering, pointed lumbar ribs are best shown

Fig. 23. *Amphibamus grandiceps* Cope. The anterior caudal vertebrae in an SEM photomicrograph of a cast, lateral view, YPM 795, × 30.

on the cast of USNM 4461 (Fig. 24), as described by Carroll (1964). Their elongated, joined heads exceed the length of the transverse processes, and the heads must have articulated with the intercentra, although there are no visible facets for them.

Both sacral ribs of *A. lyelli* are visible on USNM 4461, one edgewise and the other broadside. The edgewise one shows a definite angle just distal to the head and has a prominent knob or excrescence on the dorsum of the angle (Fig. 24). The unfused knob is rough or incomplete on the side toward the ilium. The other specimen shows that the ribs are slightly flattened. The visible sacral rib of AMNH 2002 is shorter and thicker than those of USNM 4461 and is also angled distal to the head. A poorly preserved right sacral rib can be seen on AMNH 6841.

A well-preserved sacral rib of *A. grandiceps* is visible on YPM 794 on the dorsal half-nodule. This rib is flattened in the plane of the rib heads and uniformly curved from end to end. Another example is preserved on YPM 795, divided longitudinally between the two nodule halves. It is deeper dorsoventrally and more strongly curved than that of YPM 794. I have not been able to identify sacral ribs on FMNH UC 2000.

Carroll (1964) found five postsacral ribs on one side of AMNH 6841, with the last one very short. Two caudal ribs lie along the tail on AMNH 2002. These ribs are curved in the proximal third of their length and are straight-shafted distally.

Fig. 24. *Amphibamus lyelli* (Wyman). A cast of the lumbar vertebrae and ribs, sacral rib, and half pelvis of USNM 4461, × 3.

A few caudal ribs are present on YPM 794. Those that seem to be in place are angled posteriorly and stand away from the tail at a 45° angle. Distal to the head, the caudal ribs are straight-shafted. One of the last pair is visible on FMNH UC 2000. This rib is short and smoothly curved. A third-to-last rib is visible as well, one and one half times as long, and less tightly curved.

Girdles.—The pectoral girdle has been so well described by others that there is very little to be added. The well-preserved clavicle of FMNH UC 2000 resembles that of *Dendrerpeton acadianum* as figured in Carroll (1967a:fig. 12C). Its interclavicle is more like that of *Eoscopus* in shape and ornamentation, although it is not square posteriorly.

In *A. grandiceps* the iliac blade is narrow and extends posteriorly, as Watson (1940) described it. An ilium is preserved on YPM 795, lying near the posterior portion of the vertebral column. Gregory (1950) believed it to be part of the ventral plate, but further preparation revealed that Moodie (1916) was correct in identifying it as an ilium. The dorsal part of this ilium is twice as long as that preserved on FMNH UC 2000. It is a flattened rod with a posterior edge or crest. At midlength the ilium curves dorsally and its dorsal portion curves slightly laterally.

The iliac blade in *A. lyelli* is straight, tall, uninflected, and widens dorsally. Each of the three ilia in the collection is individually recognizable. Those of AMNH 6841 and 2002 are inclined a little posteriorly relative to the ventral edge of the pelvis. AMNH 2002 is narrow, even diminishing slightly near its dorsum, whereas AMNH 6841 widens rapidly dorsally. On USNM 4461, the iliac blade rises posterior to the acetabulum and has a distinct *Eryops*-like posterior notch. Although it is possible that the *A. grandiceps* form of ilium might mature into the *A. lyelli* form, in temnospondyls the iliac blade does not change radically through ontogeny.

Limbs.—The humerus of *A. grandiceps* has a deltopectoral crest projecting at right angles to the long axis of the bone, as in *Eoscopus* (YPM 795 and FMNH UC 2000). On YPM 795, a depression is present in the ends of the crests, which according to Watson indicates that they ended in cartilage.

The phalangeal formula of the manus is 2–2–3–3 for both species (Carroll, 1964) (AMNH 6841 and FMNH UC 2000). Watson said that the second toe was the longest on the front foot of FMNH UC 2000, but the third toe is the longest, as depicted in his Figure 10. The third toe is also the longest on AMNH 6841.

Amphibamus specimens generally lack a complete adductor flange on the femur. Carroll, in his description of *A. lyelli*, reported the presence of an adductor flange only on the proximal half of the femur. The adductor flange of specimen AMNH 2002 extends most of the length of the bone. This specimen is larger and more completely ossified than any other.

The tarsi of AMNH 2002 are completely ossified, but neither is whole and the bones are vague shapes on the cast. Apparently *Amphibamus* has a complement of ankle bones similar to *Eoscopus* and *Acheloma*. The only difference is that *Amphibamus* has a horizontal bar beginning on the tibial side and extending across to the distal tip of the fibulare. Hook and Baird (1984) interpret this bar as the tibiale. Alternatively, it could be a fusion of the tibiale and intermedium.

The phalangeal formula of the pes differs between the two species. The right rear foot of YPM 794 is almost complete, lacking only the terminal phalanx of the fourth toe. The formula for *A. grandiceps* is 2–2–3–4–3, as reported by Moodie. The count for the type of *A. lyelli* is 2–2–3–?–?. AMNH 2002 has part of a foot, with the first, third, and last toes entire. The counts for these are 2, 3, and 4. Hook and Baird plausibly gave the formula for *A. lyelli* as 2–2–3–4–4. Toe length in the pes of YPM 794 varies markedly. The two inner toes are comparatively short and the three outer ones long. The longest toe, the fourth, is four times as long as the first.

The terminal phalanges of *Amphibamus* are angled ventrally at their ends. They resemble those described for *Doleserpeton* (Bolt, 1969), except that *Amphibamus* unguals are not expanded fanwise distal to the angle. This feature of the toes is most easily observed on USNM 4461 (Fig. 25). In *A. lyelli*, the unguals turn ventrally at a right angle and are square-ended. Carroll described the terminal phalanges of AMNH 6841 as being bluntly pointed and that is their appearance in a dorsal impression. The lateral aspect of a toe is visible near the edge of the slab.

In *A. grandiceps*, the terminal phalanges turn ventrally at an obtuse angle. An example of a termi-

nal phalanx is on the dorsal cast of YPM 794, where a front toe lies close to the vertebral column. Watson (1940) described FMNH UC 2000 as having claw-like unguals and the complete manus with this specimen does have sharp, curved terminal segments.

Dermal structures.—Both *A. lyelli* and *A. grandiceps* possess palpebral ossicles (Carroll, 1964). Those of *A. grandiceps* are smaller, relative to the size of the orbit, than those of *A. lyelli*. The free border of the upper eyelid in *A. grandiceps* is bounded by a row of larger, straight-edged ossicles. In addition, *A. grandiceps* appears to have ossicles in the lower eyelid and its eye opening is smaller than the diameter of the orbit. Both YPM 794 and FMNH UC 2000 preserve portions of their palpebral cups. Moodie (1916) described one as a patch of thick scales lying near the right orbit of YPM 794.

All three nodule specimens preserve large coherent patches of body scales. Like *Eoscopus, Amphibamus* was completely covered with scales in life. Watson (1940) described the ventral squamation of FMNH UC 2000 as a plastron composed of quadrangular scales arranged in chevrons. The anterior scaled area, described as fitting against the interclavicle with rows running anterolaterally, is so faintly impressed that its existence is uncertain. Chevron scale rows however, are very clearly visible on both nodule halves. Each arm of a chevron runs posterolaterally from an anterior keystone scale which Watson described as having a convex anterior and concave posterior border.

The lateral scales are anteroposteriorly narrow and imbricate, with free posterior borders. Watson's plastron may really represent the posterior belly, inner side of a thigh, and base of the tail. It is too short to cover the whole length of the trunk.

The scale patch of YPM 795 lies along the side of the vertebral column, as drawn in Gregory (1950). Median scales are present far anteriorly, close to the vertebrae, suggesting that the patch of scales is midline to lateral in position. Anterior to the visible median scales, the rows of scales run anterolaterally, suggesting that this patch of scales is from the ventral chest region. The concentric grooving that Gregory observed on these scales can be seen on both YPM 795 and YPM 794, but more clearly on the former. The grooving is shallowly curved, because the scales are nearly straight-edged. The scale patch of YPM 794 shows what appears to be half of the pectoral region.

Milner (1982) suggested that *A. lyelli* lacks scales, because none had been reported with Linton specimens, which are otherwise well-preserved. How-

Fig. 25. *Amphibamus lyelli* (Wyman). A cast of the anterior vertebrae, ribs, and front toes, USNM 4461, × 3.

ever, belly scales have since been detected by Hook and Baird (1984) associated with AMNH 2002 and *A. lyelli* has accordingly been reconstructed with scales like those of its congener (Fig. 26).

Tersomius Case 1910

Tersomius texensis was described by Case (1910) from a small skull, AMNH 4719, from the Lower Permian Belle Plains Formation. Other skulls have been assigned to *T. texensis* from both lower (Putnam, Moran) and higher (Clyde) stratigraphic levels.

In 1969, Bolt published his description of *Doleserpeton annectens,* an apparently aberrant member of the superfamily Dissorophoidea. Its diagnostic characters, bicuspid pedicellate teeth and cylindrical unitary pleurocentra, uniquely linked this Paleozoic genus with modern amphibians. Bolt later found that these characters were present in small specimens of *T. texensis,* and suggested that *Doleserpeton* might eventually prove to be a species of *Tersomius* (Bolt, 1977, 1979). *D. annectens* remains distinct from *Tersomius,* because it lacks an ectopterygoid and an internarial pit at the front of the palate. It is otherwise very similar to species of *Tersomius,* and is considered in this section along with them. Specimens are not at hand, but *D. annectens* has been thoroughly described.

T. mosesi was established by Olson (1970) from predominantly skull remains found in the Hennessey Formation (Vale or Choza equivalent) near Norman, Oklahoma. This species was founded on dentitional differences; *T. texensis* has 45–50 teeth per half jaw (Carroll, 1964), whereas *T. mosesi* has 30–35 (Olson, 1970). The teeth of *T. mosesi* are monocuspid and laterally compressed (Bolt, 1977). There are also differences in the relative proportions of their vertebral central elements (Olson, 1970; vide infra).

T. graumanni was described by Boy (1980) from a single fragmentary specimen from the Lower Permian of Germany. So little of it is preserved that it does not add much to our knowledge of osteology.

Young specimens of *Tersomius* are a common constituent of the fauna at South Grandfield, Oklahoma, probably a Clyde equivalent locality (Simpson, 1979). These were used for the present study of *Tersomius*. Most specimens are halves and quarters of skulls, but a few entire skulls and series of articulated bones are available as well. The Grandfield *Tersomius* was assigned tentatively to *T. texensis,* although these individuals are smaller than most other known examples of *T. texensis* (30 mm maximum skull length). Bolt (1977) concurs with this assignment.

The collection of *T. mosesi* from Norman was also examined. Skull size is a little smaller (about 25

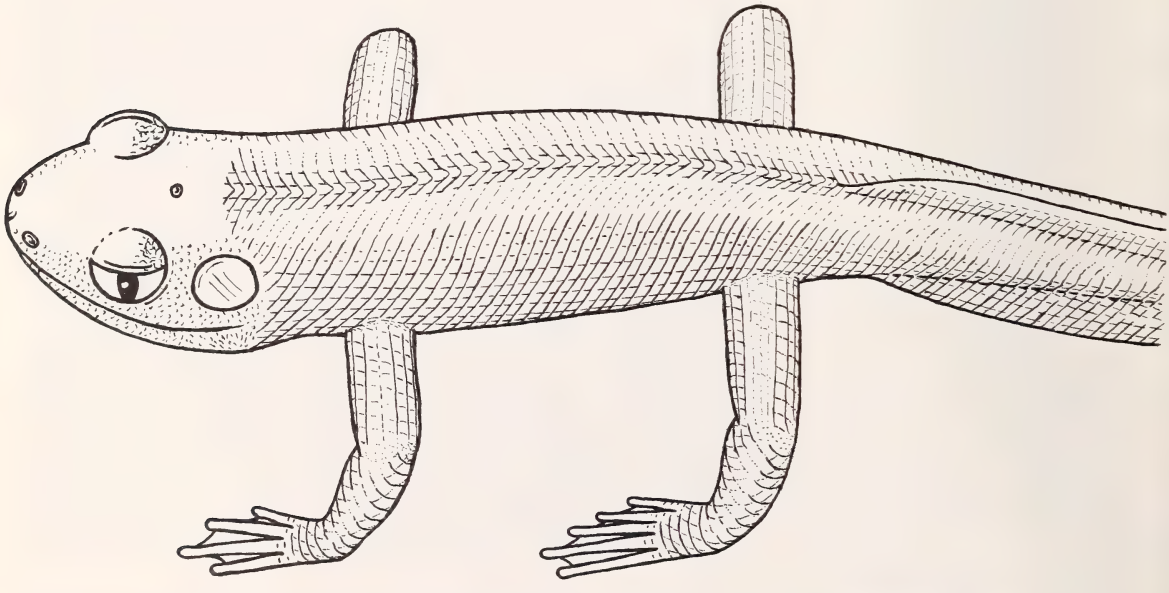

Fig. 26. *Amphibamus lyelli* (Wyman). Reconstruction of appearance in life, based on AMNH 6841. × 1.

mm maximum length), but larger than that of *Doleserpeton* (about 20 mm maximum skull length).

Neither South Grandfield nor Norman have produced any remains recognizable as pieces of dorsal dermal armor, therefore Carroll's opinion that *Tersomius* was unarmored is supported.

Specimens examined are listed below.

T. texensis from South Grandfield:

FMNH UR 1324. Posterior part of skull with anterior vertebrae and ribs; pelvis, femur, and posterior vertebrae.
FMNH UR 1329. Occipital region of skull and parasphenoidal plate.
FMNH UR 2273. Complete skull.
FMNH UR 2274. Series of vertebrae.
FMNH UR 2275. Skull fragments.
FMNH UR 2285. Jaw fragments.
FMNH UR 2286–2292. Skull fragments.
FMNH UR 2338–2342. Skull fragments.
FMNH UR 2343. Complete skull.
FMNH UR 2344–2352. Skull fragment.
FMNH UR 2353. Complete skull, laterally compressed.
FMNH UR 2354–2355. Skull fragments.
FMNH UR 2356–2357. Skulls.
FMNH UR 2358. Series of four vertebrae.
FMNH UR 2359–2362. Skull fragments.
FMNH UR 2363. Series of vertebrae.
FMNH UR 2364. Skull fragment.
FMNH UR 2365–2367. Skulls.
FMNH UR 2368–2370. Skull fragments.
FMNH UR 2371. Skull without mandible.
FMNH UR 2372–2381. Skull fragments.
FMNH UR 2386. Femoral fragments.
FMNH UR 2410. Pelvis, femora, vertebrae, and sacral ribs.
FMNH UR 2411. Posterior limb bones.

T. mosesi from Norman:

FMNH UR 1214. Fragmented skull with vertebrae and part of pectoral girdle (holotype).
FMNH UR 1215. Skull fragment.
FMNH UR 1216. Nasal and limb bone.
FMNH UR 1217. Jaw fragment.
FMNH UR 1218. Half skull.
FMNH UR 1219. Skull.
FMNH UR 1220. Skull and three vertebrae.
FMNH UR 1221–1223. Jaw fragments.
FMNH UR 1224–1225. Skull fragments.
FMNH UR 1226–1229. Jaw fragments.
FMNH UR 1251. Skull.
FMNH UR 1285. Jaw fragment, humerus, and distal end of femur.
FMNH UR 1286. Jaw fragment.
UCLA VP 2899. Partial skull.
UCLA VP 2925. Femora, tibia fragment, skull fragment, jaw fragment, etc.
UCLA VP 2928. Two series of vertebrae, ribs, distal end of humerus, and scapulocoracoid fragment.
UCLA VP 2930. Humerus fragments.
UCLA VP 2933. Skull fragments.
UCLA VP 2934. Skull, jaw, and limb bones.
UCLA VP 2995. Skull fragment.
UCLA VP 2996–2997. Jaw fragments.
UCLA VP 2998. Series of neural arches, ribs, proximal end of humerus, part of scapulocoracoid, and femur.
UCLA VP 3000. Femur.
UCLA VP 3001. Distal end of femur.
UCLA VP 3002. Partial skull.
UCLA VP 3003. Humerus and part of scapulocoracoid.
UCLA VP 3004. Skull fragment.
UCLA VP 3005. Skull with vertebrae and ribs; scapulocoracoid fragments.
UCLA VP 3006–3007. Damaged skulls.
UCLA VP 3009. Jaw fragment.
UCLA VP 3010. Skull and jaw fragments; proximal end of humerus.
UCLA VP 3011. Posterior part of skull.
UCLA VP 3013–3015. Jaw fragments.

Skull.—Carroll's (1964) thorough description renders unnecessary any lengthy exposition. His work was based on *T. texensis* of Putnam age from Archer City, but also applies to the South Grandfield and Norman skulls. Discussion will concentrate on features of interest in the *Tersomius* skull and distinctions not previously noted, like the description of *Amphibamus*. Skull measurements are provided in Table 4.

A remarkable feature of *T. texensis* is its intermandibular ossicles, small angular bones fitting closely together to armor the floor of the mouth. Examples can be seen on FMNH UR 2277, 2338, 2341, and especially 2348. The ossicles are smooth-surfaced on the South Grandfield specimens, but those from Archer City have typical surface ornament on their ossicles. The ossicles are usually four-cornered, appearing as squares, diamonds, and variously proportioned trapezoids. Marginal ossicles are often triangular. Intermandibular armor also occurs in *Micropholis* (Huxley, 1859) and *Zatrachys*

(Langston, 1953). It has recently been detected in *Dendrerpeton* (Godfrey et al., 1987).

Sclerotic plates are unknown. Palpebral bones are found whenever the whole orbit is preserved. These are squarish bones in varying sizes with an irregular arrangement. UCLA VP 3005 has a complete palpebral cup in each orbit (Fig. 27).

The parietal foramen is not always visible. Three specimens show it: FMNH UR 2371, 2377, and UCLA VP 3005. On the other specimens it may be too small to see.

The jaw articulation of *T. texensis* resembles *A. grandiceps,* and *D. annectens* as described by Bolt is even more like (it is not possible to determine the condition in *T. mosesi*). The quadrate in posterior view is three-pronged, with the dorsomedial arm serving as a dorsal process, although it is better described as the raised end of a ridge. The ventromedial arm supports part of the jaw articulation and the lateral arm completes the articular surfaces. The lateral arm is noticeably shorter and more slender than the other two in *Tersomius.* On the dorsolateral side of the dorsal ridge, a rugose attachment area is exposed between the squamosal and quadratojugal. On *D. annectens* this area is an unossified depression (Bolt, 1968). This and other features of the quadrate are visible on FMNH UR 2284 (Fig. 28). The quadratojugal covers most of the quadrate and sends a narrow posteromedial process up the dorsal process of the quadrate. The quadratojugal does not wrap around a quadrate knob as in *Eoscopus* and *D. annectens.* Just anterior to the dorsal process of the quadrate, the quadratojugal and squamosal are withdrawn from the pterygoid, exposing the attachment area of the quadrate.

The quadratojugal of *D. annectens* covers the lateral side of the quadrate but is not involved in the jaw articulation (Bolt, 1968). In *T. texensis* from South Grandfield however, the quadratojugal definitely participates in the lateral part of the condylar surface. The lack of length and thickness of the lateral arm of the quadrate is made up by the quadratojugal. The two bones are naturally positioned on FMNH UR 1324 and 2350. On some disarticulated quadratojugals, the condylar part is visible as a bump on the medial face of the posterior edge of the bone. The complete posterior part of the quadratojugal is preserved on FMNH UR 2379 (Fig. 28).

Two dissorophoidean characters, the ventral prefrontal process and the laterally exposed palatine, are present in all known populations of the genera in this family. Bolt (1974b) was unable to confirm the presence of the laterally exposed palatine for *T. mosesi,* but it is observable on UCLA VP 3002 and 3005. In *Tersomius* from South Grandfield, the palatine is often confined to the lower rim of the orbit. Of ten specimens showing this area, the palatine is only exposed as part of the rim in five and in the other five, the palatine also forms a small portion of the

Table 4. Selected skull measurements of *Tersomius* in cm.

Specimen number	Skull length	Muzzle length	Orbit length	Skull table length	Skull table width	Skull height with jaw
T. texensis						
FMNH UR 1324	—	—	—	0.4	0.9	—
FMNH UR 2273	1.4	0.4	0.5	0.5	0.9	—
FMNH UR 2343	1.2	0.3	0.5	0.4	0.8	—
FMNH UR 2346	1.25	0.4	0.3	0.6	—	0.4
FMNH UR 2353	2.2	0.8	0.8	0.6	—	0.7
FMNH UR 2356	1.4	0.5	0.5	0.4	1.0	0.4
FMNH UR 2366	1.4	0.5	0.4	0.4	1.1	—
FMNH UR 2367	1.35	—	—	0.4	—	0.4
FMNH UR 2371	1.3	0.45	0.50	0.35	—	0.4
FMNH UR 2377	—	—	—	0.4	0.9	0.4
T. mosesi						
UCLA VP 3005	1.5	0.45	0.60	0.45	1.2	0.5

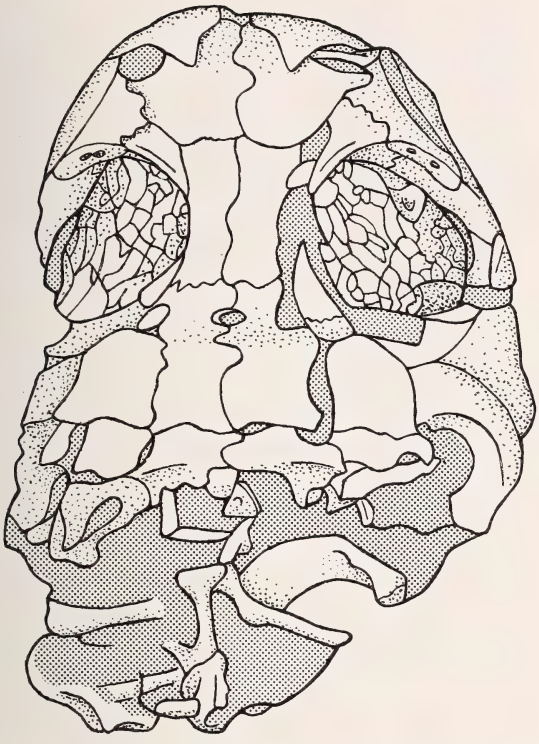

Fig. 27. *Tersomius mosesi* Olson. The skull and anterior trunk of UCLA VP 3005, × 4.

skull surface below the orbital rim.

Tersomius possesses the typical pointed premaxillary processes fitting into triangular nasal notches expected of dissorophoids. The bony floor of the nasal notches is exposed on FMNH UR 2340, 2345, 2355, and 2381. Its free edge extends from the anteriormost medial side of the notch to the middle of the lateral side, resulting in a laterally perforated notch (Fig. 29).

The internarial fenestra is like that depicted for *D. annectens* (Bolt, 1969) and may be observed on FMNH UR 2345, 2370, and UCLA VP 3002. On FMNH UR 2362, the medial borders of the premaxillae curve around a nearly circular opening, which would be round if the nasals did not dip into it from above. On FMNH UR 2340 the nasals do not participate in the borders of the fenestra at all.

Supratympanic flanges do not occur in the material examined. Bolt (1974c) however, reports the presence of a slight, straight-edged supratympanic flange in two large Archer City *Tersomius* skulls, MCZ 1912 and 1415.

The internal nasal flange, a uniquely dissorophoidean character, is present in *Tersomius* from Archer City (Bolt, 1974a), *T. graumanni* from Europe (Boy, 1980), and *Tersomius* from South Grandfield. Its anteromedial end is not exposed on any of the specimens. An end of a snout with the lateral bones missing, FMNH UR 2340, shows part of it. In this preparation, the ventral part of the nasal flange is hidden by an ascending vomerine flange that extends from the medial side of the internal naris. The two flanges come into close contact posteriorly, possibly due to dorsoventral compression of the snout. This is well shown in a posterior view of the specimen (Fig. 29). A cross-section of the right half of the snout can be seen on this

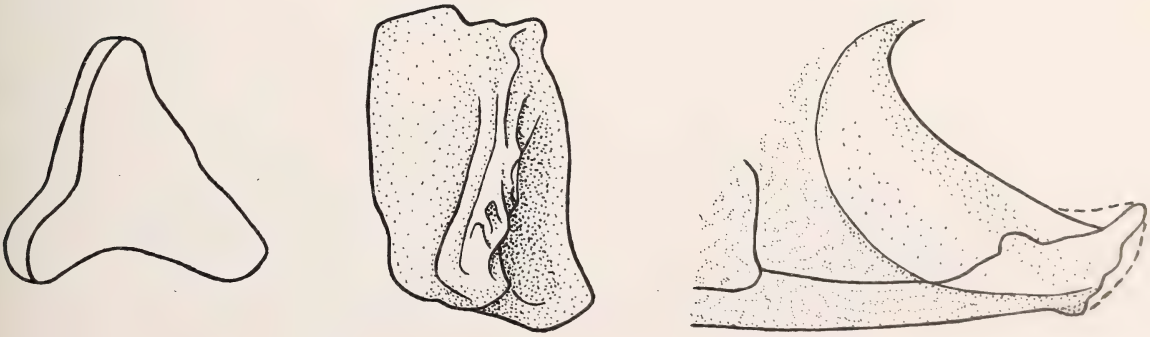

Fig. 28. *Tersomius* cf. *T. texensis* from South Grandfield. The quadrate and quadratojugal. Left: the relations of the quadrate and quadratojugal in posterior view, FMNH UR 2379, × 16.5. Middle: the quadrate in dorsal view, FMNH UR 2284, × 15. Right: the relations of the squamosal and quadratojugal in the otic notch, FMNH UR 2379, × 6.

specimen also, cutting through the internarial pit. The vomers contact the nasals near the midline of the snout here. FMNH UR 2292 shows a slightly more posterior cross-section of a snout, where the middle of the pit does not quite reach the roof. This section closely resembles the section of *Acheloma* in Bolt (1974a:fig. 3C). Here the ascending and descending flanges do not touch each other. Appressed flanges from the prefrontal and lacrimal continue the nasal flange along the ventral side of the prefrontal–lacrimal suture line, as in *D. annectens* (Bolt, 1974b). On specimens FMNH UR 2339 and 2381, the bones of the snout are separated between the nasal and prefrontal and the lacrimal. This slot has been prepared to show the descending flanges (Fig. 29). A lateral nasal flange begins at the external naris and follows the edge of the bone. The lacrimal flange contacts this flange anterior to its contact with that of the prefrontal. The ridge inside each side of the snout bifurcates at the prefrontal–nasal contact, with one limb continuing anteriorly and the other passing toward the anteromedial corner of the nasal.

The skull table terminates posteriorly in a straight transverse ridge, which is paralleled by another ridge just ventral to it on the occipital surface. This feature, which is similar to the grooved ridge of *Eoscopus,* can be seen on FMNH UR 1251 from Norman. *T. mosesi* has short tabular horns, like *Eoscopus*. UCLA VP 3011 shows the best example of tabular horns; they are square-ended like those described for *Dendrerpeton* (Milner, 1980a). Tabular horns have not been observed on any specimen of *T. texensis.*

The palatal dentition has been discussed by Bolt (1977). Carroll (1964) described *T. texensis* as lacking parasphenoidal denticles. Bolt reported that he found remains of a raised triangular denticle field at the base of the rostrum on two of the older specimens. This morphology is similar to *D. annectens* and *Tersomius* from South Grandfield. Bolt was unable to confirm the existence of the denticle field for *T. mosesi,* but it is present on UCLA VP 3004. The raised anterior corner of the field is missing, but the posterior part of the triangle is visible as a pitted

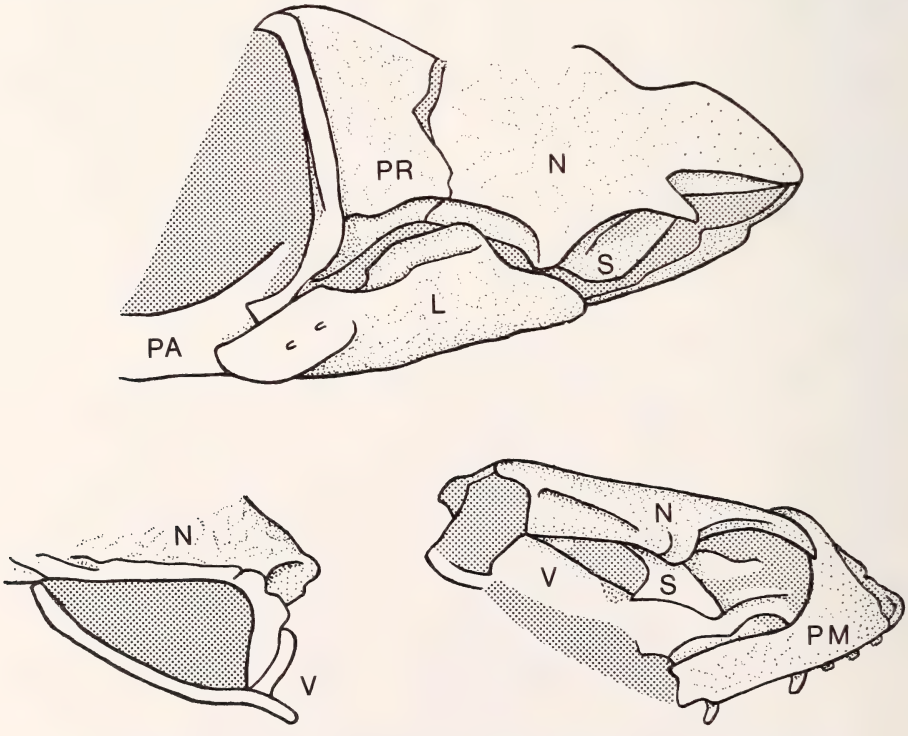

Fig. 29. *Tersomius* cf. *T. texensis* from South Grandfield. The internal structures of the muzzle. Above: a dorsolateral view of FMNH UR 2381, approx. × 8.6. Below left: a right posterior view of FMNH UR 2340, approx. × 9. Below right: the right side of FMNH UR 2340, approx. × 9.

area where the denticles have been removed.

The basicranial articulation of most *Tersomius* is like that of *Eoscopus*. The internal processes of the pterygoids are hollow cones with posterior V-shaped gaps. The processes are attached to the anteroventral edge of a large lamina ascendens, as in *Eoscopus*. FMNH UR 2364, 2379, and UCLA VP 3004 clearly show this relationship. In *D. annectens* this portion of the pterygoids has the same type of construction (Bolt, 1968), although published restorations of the joint look conventional. The exception is *Tersomius* from Archer City, which has an internal process like that of *Amphibamus grandiceps,* with a widely open posterior gap (Carroll, 1964).

In *Tersomius* the internal carotid foramina are lateral to the denticle platform and can be seen in ventral view. The anterolateral corners of the parasphenoidal plate evert and curve with the ventral sides of the basisphenoid processes formerly above them. FMNH UR 1329 shows this well.

There are three epipterygoids of *Tersomius* from South Grandfield. FMNH UR 2368 has a whole epipterygoid, although part of it is covered by the parasphenoidal rostrum. An epipterygoidal base is on FMNH UR 2276 and a base with part of a shaft on FMNH UR 2364. None of these is in its original orientation. As in *Eoscopus,* the epipterygoid does not participate in the basal articulation because the palatoquadrate cartilage was entirely surrounded by the pterygoid cone. The epipterygoid consists of a heavy rectangular base and an unbranched ascending shaft. The base bears two articular surfaces, one for the basipterygoid process and one for the otic process. The bases of the three preserved epipterygoids vary greatly in shape (Fig. 30).

The proximal parts of both stapes are present on FMNH UR 1329. There is a small foramen through the base of each, eccentrically placed.

Lower jaw.—Numerous jaw segments exist in the collections. Most of the posterior jaw fragments from South Grandfield bear a deeply-incised sculpturing on the angular and surangular. Posterior to the sculptured area, and separated from it by a definite step, is a smooth strip for the pterygoideus insertion. The edge of the step begins anterior to the angle of the jaw, rises parallel to the posterior edge, and then rounds with the dorsal corner of the lower jaw (there is no retroarticular process). Within the sculptured area, the ridging radiates dorsally from the angle. The existence of these features cannot be confirmed for *T. mosesi*.

Axial skeleton.—A vertebral count is possible only for *D. annectens,* which is estimated to have 25 presacrals (Bolt, 1969). The vertebrae of this species were described by Bolt (1968). A few vertebral specimens with the expected morphology are available in the Grandfield and Norman collections. *Tersomius* of South Grandfield has two pairs of sacral vertebrae, while *D. annectens* has one, as do most temnospondyls.

The atlas and axis are the only vertebrae definitely in articulation with *Tersomius* skulls. FMNH UR 1324 bears the posterior part of a Grandfield skull with the atlas and part of the axis posterior to it, exposed dorsally and laterally. Another atlas is present on FMNH UR 2357. The single centrum is wider than high and has a dorsomedial groove. Anteriorly, it flares dorsally to a prominent corner on each side (Fig. 31). The pedicels are fused to the centrum and each bears an arm that extends posterodorsally at a low angle. These two posterior arms lie on either side of the long ridge that remains of the axial neural spine. Posterior zygapophyses independently project from the pedicels ventral to the posterior arms, unlike those of *D. annectens,* which are borne on the arms themselves (Bolt,

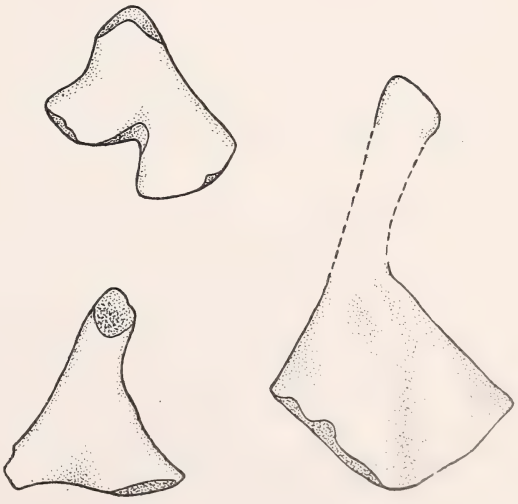

Fig. 30. *Tersomius* cf. *T. texensis* from South Grandfield. The epipterygoid, × 15. Left upper: FMNH UR 2276. Left lower: FMNH UR 2346. Right: FMNH UR 2368. Dashed lines indicate where the epipterygoid is hidden by another structure.

1968). Anterior zygapophyses have not been observed. The type of *T. mosesi,* FMNH UR 1214, appears to have an atlas posterior to its skull, exposed in ventral view. This atlas is a curving band of bone, with a concave ventral profile. A lateral view is available on the right side of UCLA VP 3005. It resembles the atlas of FMNH UR 1324.

FMNH UR 2274 from South Grandfield consists of two series of dorsal vertebrae with their parts somewhat disarranged. They have long ventral extensions of the pleurocentra, like *Eoscopus* and *Amphibamus* (Fig. 31). The ventral extensions are square-ended and must have abutted against each other when the central parts articulated (Daly, 1973). In lateral view, the pleurocentra are large and have long contacts above the notochord. Each pleurocentrum does not contact the succeeding neural arch, because the spaces above the intercentra intervene. The anterior half of each pleurocentrum seems to rise toward its contact with the neural arch.

Definite capitular facets are visible on the intercentra of FMNH UR 2274. On the longer of the two series they are large and round, covering most of the lateral portion of the intercentra. The intercentrum of the short series has a thickened, scallop-shaped notch on its posterior edge, just dorsal to the angle.

The arches of FMNH UR 2274 are like those of *Eoscopus* and *Amphibamus*. The posterior zygapophyses extend beyond the pedicels, borne on extensions that bridge over the relatively long centra. The articular plane is inclined mediad at about 45°, and the anterior zygapophyses face anteriorly at about 30 degrees. Neural spines are visible in profile as humps. The transverse processes are broken, but were elongated at the base and paralleled the long posterior faces of the parachordal processes. Another specimen from South Grandfield, FMNH UR 2363, consists of a series of three dorsal vertebrae. In these vertebrae, the neural arches are separated into halves. Transverse processes are preserved on this series, set vertically, and are much smaller distally than at their bases.

FMNH UR 1324 from South Grandfield bears a pelvis and three lumbar vertebrae lying against the palatal side of the skull (Fig. 32). Lumbar intercentra and pleurocentra are equally large in ventral view, and the pleurocentral halves are fused ventral to the notochord (although one is broken). The sacral vertebrae are exposed on FMNH UR 2410. They are distinguishable only by the size of their rib articular facets. The last lumbar arch, partly preserved on FMNH UR 2410, has a high, posteriorly-placed neural spine.

Four series of vertebrae or arches have been found at the Norman locality. In *T. mosesi* vertebrae the pleurocentra are ventrally extended, but in this species they are not flat-ended, but instead pointed, as in *Eoscopus*. They are anteroposteriorly shorter than in the older species and on their anterodorsal faces they are everted and curved to support the rounded neural arches (Fig. 33). As with FMNH UR 2274, these pleurocentra are separated from succeeding neural arches by spaces above the intercentra.

A good ventral view of *T. mosesi* vertebrae existed on FMNH UR 1220 before it was accidently

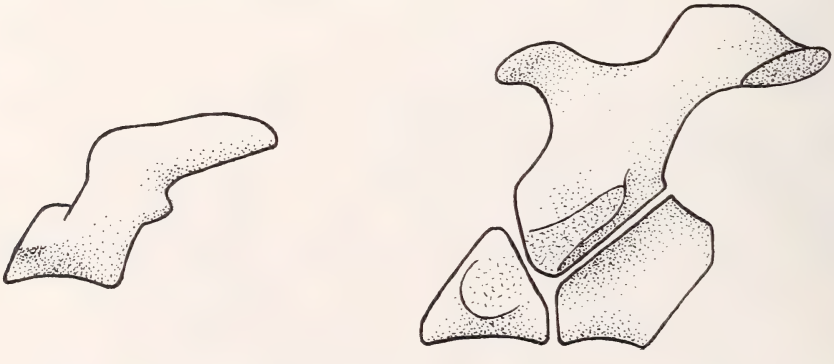

Fig. 31. *Tersomius* cf. *T. texensis* from South Grandfield. Reconstructions of the atlas and a middorsal vertebra. Left: the atlas based on FMNH UR 1324, × 16.5. Right: a dorsal vertebra based on FMNH UR 2274, × 11.25.

destroyed. The short, wide intercentra were well preserved and prepared on this specimen, including the two angulations in their posterior borders. Somewhat disarranged centra can be observed on the two series in UCLA VP 2928. On the intercentra of one of these series, a small projection points laterally from both sides, probably marking the position of the ventral borders of large capitular articular areas.

Neural arches of *T. mosesi* are preserved with the two vertebral series of UCLA VP 2928 and as a short series of isolated arches on UCLA VP 2998. The neural spines of these arches are posteriorly placed, toward the posterior zygapophyses. The articular plane is medially inclined, but only slightly anteriorly, if at all. Traces of oblique transverse processes are visible along the posterior portion of the parachordal processes.

Another series of three neural arches lies near the posterior skull segment on UCLA VP 3011. These have complete transverse processes, like those of FMNH UR 2363; they are set vertically rather than obliquely (Fig. 33). The position of these arches, behind a skull, suggests vertebral regionalism.

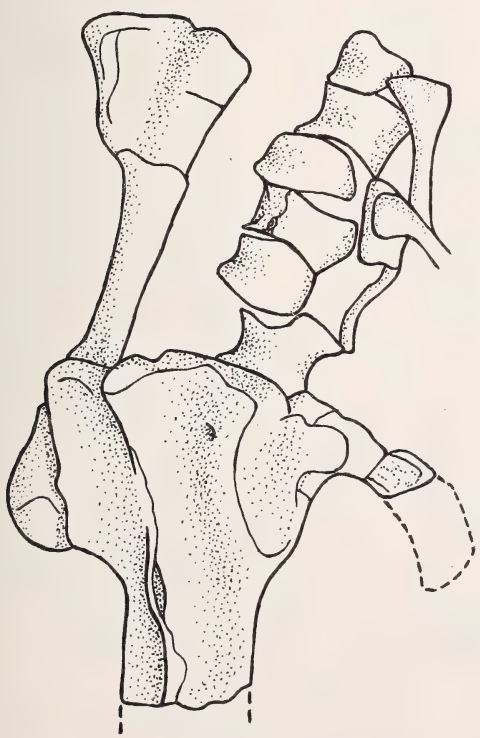

Fig. 32. *Tersomius* cf. *T. texensis* from South Grandfield. The pelvis, femur, and lumbar vertebrae of FMNH UR 1324, ventrolateral view, × 8.

Anterior caudal vertebrae are present on FMNH UR 1324 and 2410, but details are not preserved and what can be seen is not distinctive. FMNH UR 2358 from South Grandfield has four possible postsacral vertebrae. Their parts are lighter in construction than those of the other examples. These arches show a deep cleft between the anterior zygapophyses, which are set horizontally. A neural spine is present as a slight elevation dorsal to the posterior zygapophyses.

The only available description of the rib series is that of *D. annectens* (Bolt, 1968). In this species ribs begin on the axis. The first seven pairs are curved and expanded at the distal ends, with maximum expansion on the fourth pair. Subsequent pairs of ribs are straight and slender. The ribs of the sacral pair are short, thick, and striated.

FMNH UR 1324 from South Grandfield has two short thick ribs and possibly a third, near the skull on the left. Skull UCLA VP 3005 from Norman has a pair of short, strong ribs posterior to it, associated with the second vertebra. Skull UCLA VP 3011 has a row of four bones posterodorsally to it on the right, comparable in size and shape to the anterior ribs seen on other specimens. The two vertebral series of UCLA VP 2928 have ribs more or less with them, but their true length may not be preserved. Of the seven ribs associated with the series of four vertebrae, four are slim and three are thicker. The latter pass under a fragment of the scapula and are most likely shoulder ribs. Dorsal ribs have two heads joined by bone.

The lumbar vertebrae of FMNH UR 1324 have two identifiable ribs with them. They are one and one-half vertebrae long. A short thick caudal rib is preserved on FMNH UR 2410, without curvature or angulation, but it may be broken. The presumed postsacral series of FMNH UR 2358 has ribs with it, including a well-preserved, more robust rib that is about two vertebrae long.

The two pairs of sacral ribs are exposed on the right side of FMNH UR 2410 (Fig. 34). The anterior pair has a much enlarged distal blade in close contact with the anteroventral part of the ilium. The anterior blade also appears to overlap part of the pubis. It has a dorsoventrally enlarged shaft and tuberculum, and a free capitular branch. The exposed anteroventral

Fig. 33. *Tersomius mosesi* Olson vertebrae. Left: the supposed cervical neural arch of UCLA VP 3011, × 11.25. Right: reconstruction of a middorsal vertebra based on UCLA VP 2998 (arch) and UCLA VP 2928 (centrum), × 18.75.

edges are sharp, therefore the rib was not round in cross-section. The transverse process of the first sacral arch is not perfectly preserved and may not show the true shape of the end of the tuberculum. The capitulum now faces anteriorad, an indication that the proximal end of the first sacral rib has undergone a counterclockwise torsion, perhaps because of pressure from the disarticulated capitulum of the second sacral rib.

The rounded shaft of the posterior sacral rib reaches posterodorsally to bring its lengthened distal end alongside the elongate iliac blade. The distal portion of this rib resembles the narrow bowl of a spoon with a pointed end and its lateral side applied to the lower part of the iliac blade. This rib does not have a separate tuberculum and capitulum; its long, strong articular surface extends from the short tuberculum down a long, thick shaft to a flat-ended capitulum. The capitulum probably met a projecting brace on the second sacral intercentrum, which is no longer visible.

Two pairs of sacral ribs have been reported for *Cacops* (Williston, 1910), a Permian dissorophid. In *Cacops,* the distal ends of the ribs are on the same level, both contacting the iliac blade and closely pressed together to form a single articular surface. The sacral ribs of *Tersomius* do not resemble those of *Cacops* and are best regarded as an independent development.

Girdles and limbs.—Significant remains of the anterior girdle and limb have not been found from South Grandfield, so the following observations were made on *T. mosesi* from Norman.

Parts of the scapulocoracoid are associated with the skull UCLA VP 3005 (Fig. 27). The anterior part of the ventral plate exists on the right side. On the left, a piece of the articular area is the only part present. Viewed posteriorly, the articular area appears as two concave triangular surfaces, base to base; an upper, elongated posterior view of the supraglenoid buttress and a lower, more equilateral area that is the glenoid cavity.

A second left scapulocoracoid fragment, including a buttress and glenoid of similar shapes and

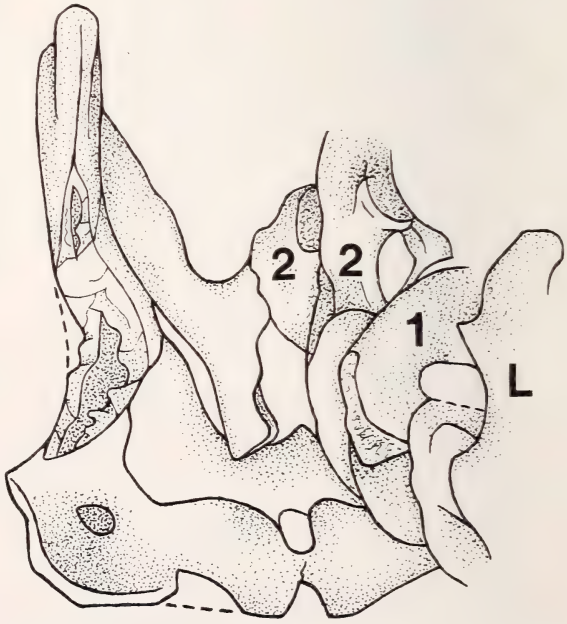

Fig. 34. *Tersomius* cf. *T. texensis* from South Grandfield. The pelvis and sacrum of FMNH UR 2410, anterior view, × 15. L = last lumbar arch, 1 = anterior sacral arch, 2 = posterior arch (broken into two parts).

proportions is present on UCLA VP 3003 (Fig. 35). This specimen revealed much more detail of the articular area. Two coracoid foramina are near the glenoid, a larger drop-shaped one and a smaller round one. A long oval supraglenoid foramen pierces the buttress. This roughly triangular glenoid cavity permitted more freedom to the humeral head than the primitive spiral strip did. However, the ventral hooked projection must have functioned as a stop to clockwise rotation of the head.

UCLA VP 3003 includes a left humerus of *T. mosesi,* rotated and a little displaced so that the humeral head is adjacent to the supraglenoid buttress (Fig. 35). This bone has a long dorsoventrally compressed shaft, with flat expanded ends, that are rotated about 45° relative to each other. A deltopectoral crest projects from the anterior edge of the humeral head about a third of the way from the proximal end. Its flat unfinished top is confluent with the anterior end of the proximal articular surface, but is slightly more dorsally oriented. The articular surface is flared toward the ventral side just proximal to the crest, where the humerus would contact the ventral stop of the glenoid. The middle part of the articular surface is widened toward the dorsal side, causing the profile of the humeral head to be concave on that side. There are no foramina in the distal end of the humerus. The unfinished end of the supinator process (on the right side on Fig. 35) is confluent with the distal articular surface.

A few other humeral ends occur in the collection. UCLA VP 2928 includes the distal end of a humerus, with a triangular supinator process that is not confluent with the distal articular surface but separated from it by a definite step.

The anterior limb and scapulocoracoid of *D. annectens* was described and figured as *Cardiocephalus* by Gregory et al. (1956), according to Bolt (1968). Its humeri are readily distinguished from those of *T. mosesi,* because those of *D. annectens* are slimmer and more ossified. Large specimens possess fully ossified distal ends. The scapulocoracoid differs in having a narrow straplike glenoid fossa, rather than a triangular one.

Two pelvis specimens are in the collection from South Grandfield (Figs. 32 and 34). FMNH UR 1324 has a well-preserved ventral plate and acetabulum, while FMNH UR 2410 has a good iliac blade. The most notable feature of these pelves is an ossified pubis indistinguishably fused to the ischium, despite the small size of these specimens. In ventral view, the puboischiadic plate is square anteriorly, but narrows behind the acetabula to three-

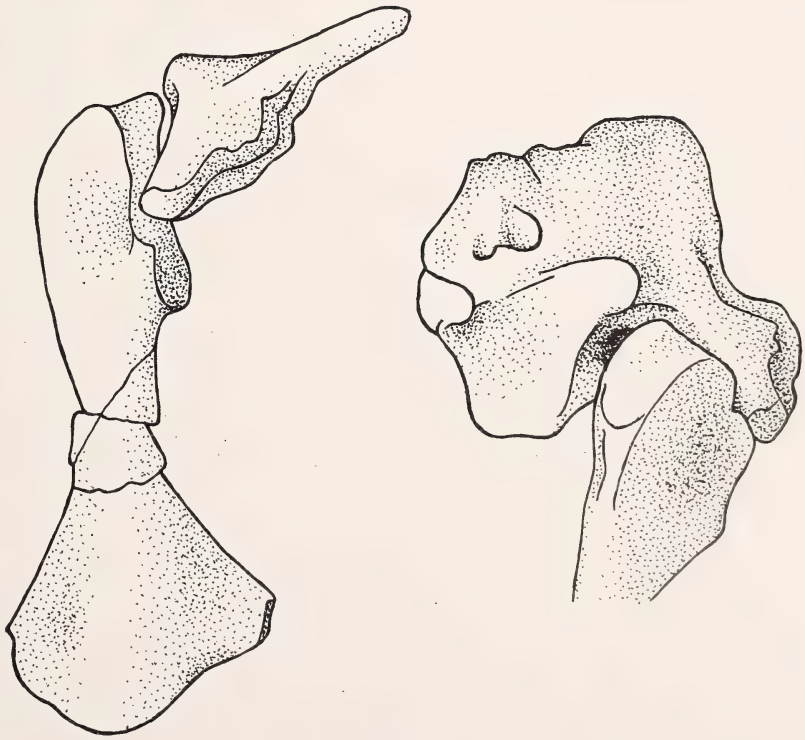

Fig. 35. *Tersomius mosesi* Olson. The scapulocoracoid and humerus, UCLA VP 3003, × 15. Left: the left humerus in ventral view, with the near part of a scapulocoracoid fragment. A broken edge of the fragment is toward the viewer. Right: the glenoid region in posterior view, and the head of the humerus.

fifths of its anterior width. The posterior end of the plate is damaged in both specimens. The acetabula are visible from below as concavities in the sides of the plate. The articular surface has a posterior notch, as expected, and a slight anterior notch in addition. There is no projecting lip above the acetabulum.

FMNH UR 2410 shows a strong eversion of the pubes. The flared borders turn ventrally and then anteriorly, such that the front of the pelvis is stepped. In ventral view, the halves of the plate meet in a wide V. On FMNH UR 1324, the anterior end of the pelvis is horizontal and the pubes are only slightly everted, suggesting that the specimen was damaged anteriorly. The medial side of the obturator foramen is visible on the pelvis of FMNH UR 2410, just dorsal to the ventral inflection. It faces anteriorly, as in *Eoscopus*. The lateral opening is preserved on the left side of FMNH UR 1324.

The iliac blade is a laterally flattened arm that extends posterodorsally in lateral view. Its posterior edge describes a smooth arc, while the anterior edge bears a prominent corner at its midpoint and a straight border to the posterodorsal corner.

Both pelves have femora in articulation. FMNH UR 1324 has a complete one and part of a tibia and fibula, but these are not well preserved. A complete, well-preserved femur is preserved with the pelvis of FMNH UR 2410. No femur in articulation has been found in the Norman collection. There are numerous femora and femoral ends in both collections, however, that are similar to the femur of FMNH UR 2410. Proximally, the femur is angular to rounded depending on the specimen, with the internal trochanter curving from one side of the head (Fig. 36). An adductor crest, rather than a flange, passes distally from the internal trochanter until it disappears just short of the popliteal space. The femur is straight and does not curve ventrally at the distal end. Fine longitudinal grooves can be seen on the distal end, especially in the intercondylar fossa on the anterior of the knee. The depth of the fossa and the angularity of the femur in end view depend on the size and extent of ossification of the specimen.

FMNH UR 2411 includes a tibia and fibula in articulation with the distal end of a femur (Fig. 37). The two bones are the same length and about 60% as long as most femora. Their expanded ends are rotated about 45° with respect to each other. The tibia is straight, with a wide, thick proximal end and a definite cnemial crest. The surface on the fibular side of the crest shows longitudinal grooves where the quadriceps tendon inserted. The fibula is strongly bowed away from the tibia. Its flat, expanded ends are at right angles to the axes of the tibial ends. A groove, probably for an artery, passes ventrally across the distal inner corner, as in *Eoscopus*.

Distal to the crus, a set of disarranged tarsal bones is present on FMNH UR 2411 (Fig. 37). The fibulare is readily identified by its size and position. Between the ends of the tibia and fibula is a square bone with a notch in one edge that must be the intermedium. There are nine other tarsals. Although this specimen does not permit a detailed description of the ankle, the complete complement of tarsal bones is present at this small body size.

The pelvis described for *D. annectens* in Gregory et al. (1956), seems very close to that of the South Grandfield animal, except that the inflected anterior parts of the pubes are always missing. As in the case of the humerus, the femur and lower limb bones of *D. annectens* are distinguished by their comparative slenderness and greater extent of ossification.

The only available descriptions of a dermal pectoral girdle, carpus, and manus are by Bolt (1968). These elements do not have any unusual features except for the terminal phalanges, whose tips are turned ventrally at a right angle and more or less expanded laterally.

Fig. 36. *Tersomius mosesi* Olson. The femur in ventral view, UCLA VP 2925, × 10.

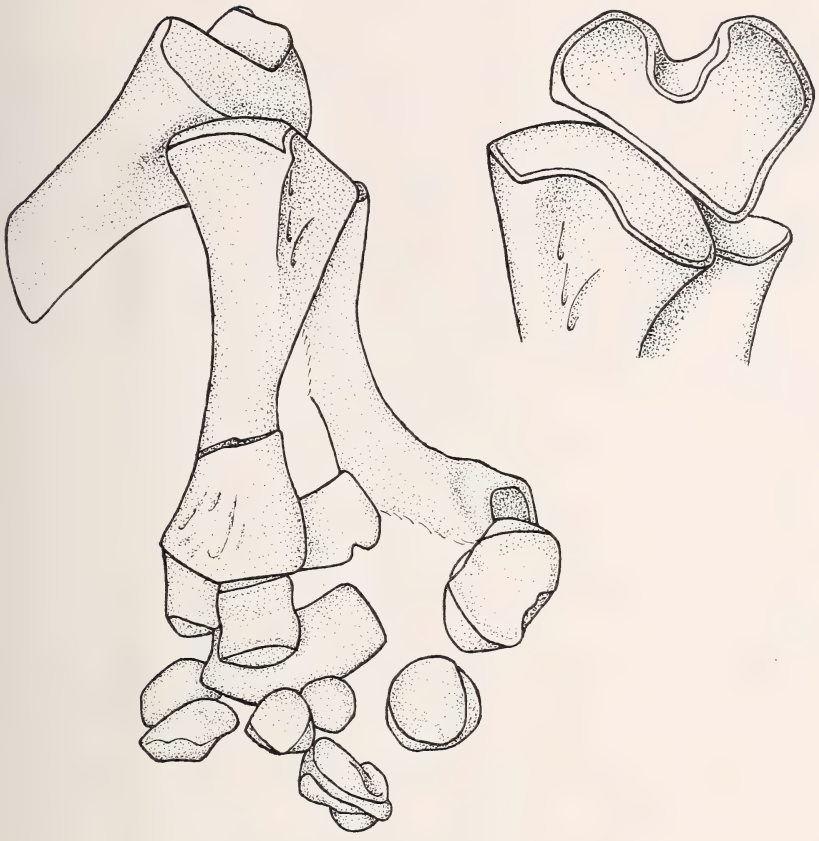

Fig. 37. *Tersomius* cf. *T. texensis* from South Grandfield. The hindlimb of FMNH UR 2411, × 10. Left: the distal end of the femur, crus, and tarsus. Right: the femur in end view and the dorsal side of the proximal end of the tibia.

The Family Amphibamidae

Eoscopus, Amphibamus, Doleserpeton, and *Tersomius* were described above as members of the new family Amphibamidae. *Micropholis stowi* Huxley 1859 is an "unspecialized dissorophid" that has not yet been considered. Specimens of this South African Triassic genus were not inspected, but the descriptions and figures of Boy (1985), Broili and Schröder (1937) and Watson (1913) reveal its amphibamid characters.

The vertebral centra of *Micropholis* resemble those of *Eoscopus* (Figs. 7, 38). The length and curvature of the ribs illustrated for the genus *Micropholis* in Broili and Schröder would seem to make familial reassignment doubtful; however, this series of ribs was conventionally restored. The plates of the specimens reveal that most ribs are either missing or not fully prepared. A figure of the four anterior pairs is available in Watson, who shows them as short and robust. His description reads ". . . the ribs are sufficiently described by Figs. 1 and 3, the more posterior ribs being similar but more slender."

Despite surviving to a late geological age, *Micropholis* retains an unfused basal articulation. The stapes of *Micropholis* is perforated by a foramen. On the whole, *Micropholis* is reasonably interpreted as an amphibamid. The one discordant feature is its large external nares, more like that of a dissorophid than an amphibamid.

Next most likely as amphibamids are the aquatic micromelerpetontids. Boy (1972) established this family with his redescription of *Micromelerpeton credneri* Bulman and Whittard 1926. *Micromelerpeton,* as Boy noted, has long pleurocentra (Fig. 38). Ventral cartilaginous extensions of the pleurocentra must have filled most of the gaps between successive intercentra; cartilaginous extensions of the intercentra could not have touched each other without encroaching upon the bony pleurocentra. As reconstructed by Boy, the pleurocentra of *Micromelerpeton* only weakly support the neural arches. According to A. R. Milner (in litt.) the pleurocentral faces of the parachordal processes are longer than the intercentral faces on the specimens he has seen. This observation brings *Micromelerpeton* still closer to amphibamid morphology.

Like the branchiosaurs, *Micromelerpeton* has short ribs. They lack the axial pair of ribs, like

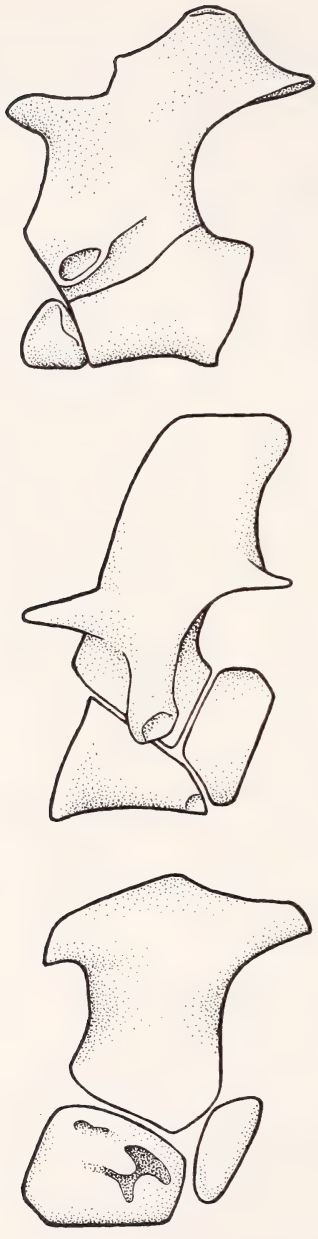

Fig. 38. Reconstructed mid-dorsal vertebrae of three proposed amphibamids. Above: *Doleserpeton,* after Bolt, approx. × 14. Middle: *Micropholis,* after Broili and Schröder, approx. × 10. Below: *Micromelerpeton,* after Boy, × 10.

Amphibamus, but this may not be an indication of relationship. The axial ribs are probably absent because of the persistence of internal gills. The reduced axial pair of ribs in branchiosaurs probably result from the same cause. The remainder of the morphology of *Micromelerpeton* conforms well to the amphibamid pattern, with small nares, a stapedial foramen, bony scales, a moveable basal articulation , and iliac blades that curve slightly posteriorly. The iliac blades resemble those of small *Dendrerpeton* (Carroll, 1967a). *Micromelerpeton* also has some notable differences, with a visible lateral-line system, a lack of internal nasal flanges, no rostral fontanelle, and 27–29 presacral vertebrae. These peculiarities, in addition to its possession of gill rakers, can be attributed to its aquatic adaptation from the amphibamid morphology.

Boy (1972) placed two other genera in the Micromelerpetontidae: *Limnerpeton laticeps* Frič 1883 from Nýřany, a contemporary of *Amphibamus,* and *Branchierpeton amblystomum* (Credner, 1881) from Niederhässlich, Lower Permian. Both of these are aquatic dissorophoids. Milner (1986) briefly reported the results of his study of the fossil tetrapods from Nýřany. *L. laticeps* is now *Amphibamus laticeps* Frič 1881. A newly distinguished dissorophoid, *Limnogyrinus elegans* (Frič, 1881) is assigned to the Micromelerpetontidae. *Mordex calliprepes* Steen 1938, once considered an *Amphibamus* (Carroll, 1964), has its own genus again. *Branchierpeton* and *Limnogyrinus* are possible amphibamids.

The status of the Branchiosauridae must be considered. A. R. Milner (1982) suggested that this family was derived paedomorphically from among or near the Dissorophidae. We cannot know the form of their central vertebral elements, because they are never ossified. The ventral portions of their neural arches are also incomplete. Branchiosaur ribs are short. However, they uniquely possess a shorter, slimmer, axial pair (Boy, 1978). Despite their paedomorphic nature, branchiosaurs lack a parasphenoidal denticle field. *B. humbergensis* and *B. tener* may have denticles on or near the rostrum, but they lack the raised platform. Their most divergent feature from amphibamids is the shape of their iliac blades: tall, straight, and slim-waisted. No dissorophoid has ilia like this; they most resemble

those of trimerorhachoids and the larval *Archegosaurus* (Steen, 1937).

Branchiosaurus does not appear to be closely related to *Micromelerpeton*. *Branchiosaurus* has a shorter back, larger limbs and reduced pectoral girdle, indicating derivation from a highly terrestrial ancestor (Boy, 1978). *Micromelerpeton's* conservatism suggests a different ancestry, one that permitted aquatic life without extreme paedomorphism, although some change in proportions has occurred.

The affinity of the branchiosaurs is difficult to determine. If they are dissorophoids, they lack the diagnostic characters of the superfamily: the laterally exposed palatine, the ventral prefrontal process, the posteromedial process of the quadratojugal, and probably the dorsal process of the quadrate as well. Although the quadrate is unossified, the last two characters co-occur in dissorophoids (Bolt, 1969, 1974b). A. R. Milner proposed that these characters were lost through paedomorphic adaptation to aquatic life. It is, however, not possible to be certain that they were ever acquired. In addition, branchiosaurs have a suite of derived characters of their own. Some of these include a low vertebral count (rare in temnospondyls), a reduced axial pair of ribs, narrow erect iliac blades, elongate subtemporal fenestrae (possibly not present in *B. caducus*), short pointed tabular horns (directed posteriorly or medially), deep jaw suspension extending anteriorly, and a reduced subotic portion of the squamosal.

In summary, the branchiosaurs are a specialized discrete group that should be classified *superfam. incertae sedis*.

The Dissorophoidea Now

The Amphibamidae can no longer be considered ancestral to the Permian families of dissorophoids, or as primitive survivors of a basal group. Their specializations of the ribs and vertebral centra make this scenario unlikely. Their primitive features, and the age of *Amphibamus*, suggest that amphibamids are an early derivative of dissorophoids and that the trematopids and the dissorophids are more closely related to each other than to the amphibamids. In the absence of new fossil material, evidence of dissorophoidean interrelationships must come from character analysis.

Recently, specific hypotheses of the relationships of the superfamily have been put forward. Godfrey et al. (1987), in their phylogeny of the temnospondyls, unite the dissorophoids to the eryopoids through an ancestor that had lost the intertemporal bone. This loss must have occurred early in the Pennsylvanian, a time when most temnospondyls possess it. Only ichthyostegids, colosteids, and *Megalocephalus* (a loxommatid) are known to have also lost the intertemporal.

Godfrey et al. (1987) next join the dissorophoid-eryopoid lineage to the edopoids and trimerorhachoids. This larger group is characterized by the loss of the entepicondylar foramen from the humerus and an impedance-matching ear for detecting airborne sound. Trimerorhachoids apparently have degenerate ears, because their otic notches are slight. However, they do have a rod-like stapes that is dorsally directed. As the largest group, these authors unite dendrepetontids with the previous group of temnospondyls, because their vomers enter the borders of the interpterygoidal vacuities. (However, reversals are known for this feature.) This hypothesis was guided by their study of a new, undistorted skull of *Dendrerpeton acadianum* from Joggins. Godfrey et al. (1987) identified the stapes of *D. acadianum* as a heavy bone bracing the jaw suspension on the braincase. An impedance-matching ear could not have been present. A stapes of this type exists in the Mississippian colosteid *Greererpeton* and these authors suggest that this state is primitive for tetrapods.

A quite different view of *Dendrerpeton* is expressed by Milner. He proposed that this genus is closely related to the dissorophoids, based on his study of *D. rugosum* from Jarrow (Milner, 1980a). Shared derived characters supporting this relationship include a high rounded otic notch, a dorsal process on the quadrate, and short tabular horns, structures that indicate the presence of a large tympanum and therefore an advanced ear. Another possible shared derived feature is the anterior reduction of the jugal, such that its center of growth lies posterior to the orbit. The form of the jugal distinguishes *Dendrerpeton*, dissorophoids, and branchiosaurs from most other temnospondyls, because this bone is normally largest ventral to the orbit. Milner (1980b) also noted that *Dendrerpeton* is replaced by *Amphibamus* in Pennsylvanian faunal assemblages between Westphalian B localities and the younger

Westphalian D.

Solving dissorophoidean relationships does not need to wait for the placement of *Dendrerpeton*. Characters with useful distribution and whose polarity could be determined were taken from the literature. These characters are necessarily dependent on other workers' descriptions and figures. The results of this analysis are presented in a phylogram (Fig. 39). This diagram continues the summary presented in Godfrey et al. (1987:fig. 5), beginning just before the topmost branching point, with character 32 (loss of intertemporal bone). *Dendrerpeton* is not considered; it does not share character 32.

Five groups of Permo-Carboniferous temnospondyls lack the intertemporal bone: Dissorophoidea, Eryopoidea, Branchiosauridae, Zatrachydidae, and Stegopidae. This hypothesis is supported by the scattered occurrence of two other acquired characters in these groups:

2. a cylindrical internal process of the pterygoid; and
3. a dorsal process of the premaxilla lapping onto the nasal, medial to the naris.

The internal process of the pterygoid is not cylindrical in *Edops* and the trimerorhachoids, although their basal articulations are too complex to be considered primitive. The process is cylindrical and open posteriorly in *Stegops* (Romer, 1930:fig. 18), and *A. grandiceps* and *Tersomius* from Archer City (Carroll, 1964). It is cylindrical and slotted posteriorly in *Branchiosaurus* and *Micromelerpeton* (Boy, 1972), *Stegops* (Steen, 1931:fig. 9), *Eoscopus, Tersomius* from South Grandfield, and *Ecolsonia* (Berman et al., 1985). Details of the basal articulation are not available for most dissorophids, because the bones participating are fused together. The immovable joint of *Kamacops* (Gubin, 1980) lies between a round bony rod on the lateral or pterygoid side and the epipterygoid, the basisphenoid, and the parasphenoid on the medial side. This round bony rod could be derived from the cylindrical internal process of the pterygoid via ossification of the palatoquadrate core. Additional evidence justifying this interpretation is the exclusion of the epipterygoid from the lateral side of the joint.

Eryops (Sawin, 1941) has a complete bony socket as its internal process, which receives a projection from the basisphenoid. The epipterygoid, which lies across the joint, bears only part of the dorsal edge of the socket. A palatoquadrate core is either absent or present as the cartilaginous termination of the basisphenoid wing. If the internal process of *Eryops* is homologous with the cylindrical internal process of amphibamids, then the derived form of the pterygoid is present in four of the five groups that lack the intertemporal.

The internal process of the pterygoid is not cylindrical in the trematopid *Actiobates*. In *Actiobates*, the process is a hemicylinder that is open dorsally. The recently described trematopid *Anconastes* shares this configuration (Berman et al., 1987:fig. 11), as does a larval trematopid (Olson, 1985) described as having a slim internal process grooved dorsally. This modified state is apparently unique to trematopids.

The third character is also present in four of the five groups. Dorsal processes of the premaxillae occur in *Eryops, Onchiodon, Osteophorus, Stegops* (Romer, 1930:fig. 17), *Zatrachys*, all known amphibamids, all trematopids but *Anconastes, Broiliellus, Conjunctio, Ecolsonia*, and *Platyhystrix*. The premaxillary processes reported for *Trimerorhachis sandovalensis* penetrate the nasals rather than lap onto them (Berman and Reisz, 1980).

The next most inclusive group depends on one character:

4. a parasphenoidal denticle field with raised anterior and lateral borders.

Some genera have a denticle patch set on the parasphenoid that is not raised from the general level: *Dendrerpeton, Edops, Eryops* (small specimens), and *Branchiosaurus* (two species). This distribution suggests that this is the primitive character state. A denticle field set on a raised surface on the parasphenoid is interpreted as a state that occurred only once. It is distributed as follows: *Stegops* (Steen, 1931), *Zatrachys* (small specimens, Steen, 1937), all amphibamids, *Actiobates, Anconastes*, larval trematopids, and *Ecolsonia*. This results in a trifurcate tree, with the Eryopoidea as one branch, the Branchiosauridae as another, and three taxa (Dissorophoidea, Zatrachydidae, and Stegopidae) as the third.

Stegops and *Zatrachys* must be left on two ends

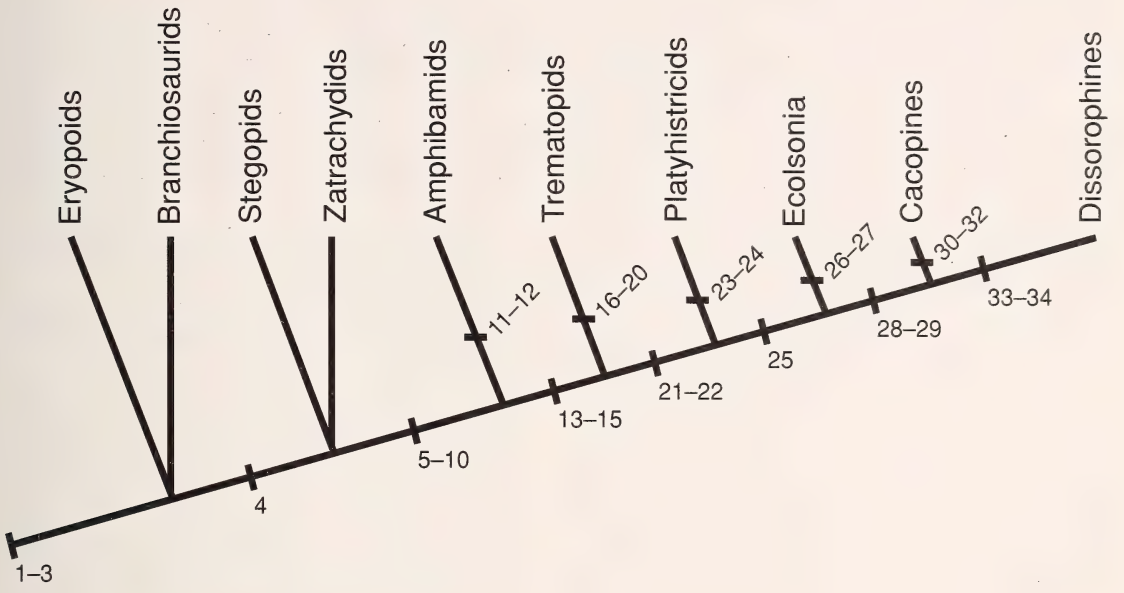

Fig. 39. A phylogram illustrating the hypothesized relationships of the dissorophoids and temnospondyls nearest to them. The numbers correspond to the characters listed in the text.

of another unresolved trifurcation. The Dissorophoidea is supported by six characters, as follows:

5. a laterally exposed palatine anteroventral to the orbit (DeMar, 1968; Bolt, 1969, 1974b);
6. a ventral prefrontal process that contacts the dorsal end of the palatine medial to the lacrimal within the orbit (Bolt, 1974b);
7. a dorsal process of the quadrate (Bolt, 1969);
8. a posteromedial process of the quadratojugal associated with the dorsal process of the quadrate (Bolt, 1969);
9. a supratympanic flange on the dorsal border of the otic notch (DeMar, 1968; Bolt, 1974c) including a supratympanic shelf and a semilunar flange of the squamosal; and
10. an internal nasal flange inside the snout (Bolt, 1974a).

The supratympanic flange is usually absent in amphibamids, but *Eoscopus* possesses it. therefore, the absence of the supratympanic flange in other amphibamids, or its slight development, is not primitive.

Within the Dissorophoidea, the amphibamids are united by the following:

11. pleurocentra that meet or approach each other ventrally; and
12. the loss of the thoracic basket.

Three characters unite the trematopids and the dissorophids and exclude the more primitive amphibamids. These are:

13. large external nares;
14. the loss of the stapedial foramen; and
15. short broad iliac blades.

External nares are usually small in adult temnospondyls and large in members of the Trematopidae and Dissorophidae. Only the geologically late *Micropholis* (large nares) and *Kamacops* (small nares) deviate from this pattern. Absence of the stapedial foramen is almost universal; it is present only in *Anconastes* (Berman et al., 1987). The foramen reported for *Actiobates* (Eaton, 1973) is actually a pit upon closer inspection.

The long, posteriorly inflected iliac blades observed in most amphibamids are considered primi-

tive, because they are found in *Dendrerpeton, Caerorhachis,* and *Pholidogaster.* A tall erect iliac blade occurs in *Eryops* and *Branchiosaurus,* possibly as a homologous character state. The iliac blades of *Amphibamus lyelli* are interpreted as a parallel modification. Short erect blades are observed for the few trematopids and dissorophids in which the pelvis is known. A rounded iliac blade was described for *Dissorophus multicinctus* (DeMar, 1968), *D. angustus* (Carroll, 1964), and *Acheloma cumminsi* (Olson, 1941, as *Trematops*). This form also appears to be present in *Actiobates,* although the upper part of the blade is cartilaginous or broken in the only known specimen. The square iliac blades of *Ecolsonia* and *Cacops* are considered modifications of the same character.

When only the Permian genera were known, the Trematopidae seemed clearly distinguished by elongated external nares, lengthened muzzle, enlarged premaxillae, reduced interpterygoidal vacuities, and short imbricating thoracic ribs. Descriptions of the Pennsylvanian genera *Actiobates* and *Anconastes* have shown that only their elongated external nares remain as a valid character to unite all four genera in a single family.

Recent work has clarified the concept of the Trematopidae once again. Now the family can be defined by a substantial suite of characters, as follows:

16. elongated external nares (paralleled in *Ecolsonia* and *Mordex*);
17. caniniform tooth on premaxilla and a pair of caniniform teeth on maxilla (Dilkes, 1990);
18. median vomerine septum inside the snout (Dilkes and Reisz, 1990; Dilkes, 1990);
19. inflection of the prearticular along the medial rim of the adductor fossa (Dilkes, 1990); and
20. hemicylindrical internal process of the pterygoid, open dorsally.

The remaining dissorophoids are at present considered members of the heterogeneous family Dissorophidae. Berman et al. (1987) presented a list of four characters, in an attempt to unite most dissorophids, after first removing *Amphibamus, Tersomius* and *Doleserpeton* from consideration. Two of these have not been invalidated by later published observation: dorsal dermal armor plates and characteristic skull ornament. Although these two characters have long been recognized, they are not entirely satisfactory for diagnosis, because of the suspicion that they are composite. In particular, skull ornament can be divided into three characters, by observing the cases in which it is not completely present.

Two characters unite all dissorophoids beyond the trematopids:

21. exaggerated surface sculpture on the borders of the skull table and on the cheeks; and
22. replacement of the supratympanic shelf with sculpturing that covers the lateral area above the otic notch and most of the tabular.

Berman et al. (1981) used these two characters in their argument that *Platyhistrix* is a dissorophid.

The supratympanic shelf was first described by Bolt (1974c) from a trematopid skull and accepted by Dilkes (1990) as a diagnostic of the family. Now that *Eoscopus* is known, the supratympanic shelf is evidently primitive in dissorophoids and its absence is derived. Its obliteration may be related to development of sculpture, and in that case it would not be an independent character. Again, loss of the shelf may be due to changes in ear anatomy, or it could be related to both factors.

Platyhistrix is the most aberrant of dissorophoids, separated by the following apomorphies:

23. a dorsal sail, composed of lengthened and laterally flattened neural spines; and
24. a characteristic nodular ornament.

Platyhistrix and *Astreptorhachis*, who share these characters, should be united in a separate family, the Platyhistricidae, fam. nov. The unusual ornament covers the surfaces of the skull, most of the neural spines, and parts of the anterior ribs (Langston, 1953). The ornament may include dermal components, but is not here considered homologous with the dermal plates of other dissorophoids.

After removal of the platyhistricids, the remaining dissorophoids share the following:

25. tabular lateral corners or horns positioned above the quadrates.

This character leads to the right-angled notch closures that are observed in this group (Bolt, 1974c). In members with closed otic notches, tabular exten-

sions drop straight downward to join upright quadrate processes.

Ecolsonia, another aberrant dissorophoid, diverges at the next node of the tree, with the following apomorphies:

26. elongated external nares, a parallelism with trematopids, and
27. high intercentra, with dorsal ends approaching each other or touching above the notochord.

Milner (1986), in his revision of the dissorophoids of Nýřany, describes *Mordex calliprepes* Steen 1938 as possessing elongated external nares, and proposes that *Mordex* is closely related to *Ecolsonia*. The neural spines of *Ecolsonia*, with their nodular tops and lateral knobs, could indicate close relationship with *Platyhistrix*. This genus should be left *incertae sedis* for the present.

After removal of *Ecolsonia*, the remaining dissorophoids share the following:

28. characteristic lateral ridges on the skull, extending from a circumorbital ridge; and
29. sculptured dermal plates associated with the vertebral neural spines.

These are long-recognized characters that define the typical dissorophids.

The skull ridge system is variously developed on both the taxonomic and individual levels, and when completely expressed includes four ridges. Two ridges extend from either end of the orbital rim. The anterior medial ridge crosses the prefrontal, follows the lateral border of the nasal, and then turns medially and anteriorly to terminate between the naris and the midline of the snout. The lateral anterior ridge leaves the circumorbital one near the prefrontal-lacrimal suture line, ascends to near the medial ridge, and thence runs forward to the rim of the naris along the medial border of the lacrimal. The course of the lateral ridge near the orbit creates an apparent triangular depression on the prefrontal. The posterior medial ridge crosses the postorbital and follows the edge of the skull table, while the posterior lateral component originates lower on the orbit and ascends to merge with it or run parallel with it. Another triangular depression is created on the postorbital to match the prefrontal one.

The dorsal dermal plates are so varied in their morphology that dissorophid phylogenies have been based on details of their form, arrangement and relations with the neural spines. DeMar (1966b) concluded that the plates had evolved at least twice within the family. He called the two lines the Dissorophinae and the Aspidosaurinae, perpetuating names originally proposed by Williston (1914) on other grounds. Carroll (1964) produced an armor-based phylogeny that subdivided the family in an entirely different way. Bolt (1974d) cast doubt on the suitability of the dorsal armor for phylogenetic analysis, given our limited knowledge of individual variation.

The Dissorophidae can be divided further without utilizing features of the dorsal dermal plates. DeMar (1966b, 1968) defended the reality of his Dissorophinae by contrasting other characters of *Dissorophus* and *Broiliellus* with those of *Cacops*, the exemplar of his Aspidosaurinae. He noted their differences in skull depth, skull surface ornament, number of sacral ribs, and anteroposterior level of the jaw articulation. When *Cacops* is compared with contemporary dissorophids, it is set off by the following:

30. two sacral rib pairs;
31. slim ribs without uncinate processes; and
32. loss of exaggerated surface ornament on the cheeks and edges of the skull table.

Most dissorophids have one sacral rib pair, so far as we know. Their dorsal ribs are slatlike with uncinate processes in the thoracic region. *Eryops* has similar ribs, so the ribs of dissorophids are regarded as primitive retentions. The surface of the skull of *Cacops* is covered with a uniform coarse ornament, but retains most of the lateral ridge system (Williston, 1910).

Most described dissorophids are "typical" and make up the Dissorophinae of DeMar (1966b). Their apomorphies are:

33. occipital condyles located near or at the anteroposterior level of the jaw articulation; and
34. knobby exostoses ornamenting the dorsal skull bones.

This subfamily originally contained *Dissorophus*

and *Broiliellus* (DeMar, 1966b) but *Brevidorsum* and *Conjunctio* were soon added to it (DeMar, 1968). *Aspidosaurus novomexicanus* possesses a gently concave posterior margin on its skull table (Carroll, 1964:fig. 17), indicating that its quadrates and occipital condyles lie close to each other. The same is true of *Longiscitula* (DeMar, 1966a).

DeMar's Aspidosaurinae was nominally based on *Aspidosaurus chiton* Broili 1904. Broili's figure and description of the only known skull reveal that it possesses exostoses on its dorsal bones, variation in intensity of its dermal sculpturing, and a gently concave posterior margin. Therefore, *A. chiton* is a dissorophine as defined here.

A new subfamily coordinate with the Dissorophinae should be created, based upon *Cacops aspidephorus* Williston 1910. The Cacopinae subfam. nov. can be augmented with *Kamacops* (Gubin, 1980). This Upper Permian dissorophid has a deeply concave posterior skull margin, a uniform sculpture on its skull bones, and a closed otic notch. Another possible member is *Zygosaurus*, also from the Russian Upper Permian. *Zygosaurus* is represented now only by a plaster cast of a poorly preserved skull. Efremov's (1937) illustrations of it show a dissorophoid with a closed otic notch and a deeply concave posterior margin, and it can be tentatively assigned on that basis.

A closed otic notch may be a shared derived character for cacopines, but its possible correlation with larger skull size makes it suspect. All dissorophids with a midline skull length of 120 mm or more have closed otic notches.

Not placed in the above analysis are *Iratusaurus* (Gubin, 1980) and *Fayella* (Olson, 1965, 1972). *Perryella* (Carlson, 1987) is not a dissorophoid, but could be related at zatrachydid grade.

DISCUSSION

The short ossified ribs of amphibamids are seen elsewhere in larvae (Steen, 1937; Boy, 1974) and in permanently aquatic forms. Ribs of the usual temnospondyl size and shape would undoubtedly handicap swimming movements. The functional significance of the short ribs of amphibamids is uncertain. Only *Micromelerpeton, Branchierpeton* and *Limnogyrinus* are thought to be aquatic.

Amphibamid pleurocentra are an exclusive feature among contemporary temnospondyls; by contrast, tall intercentra occur sporadically (*Trimerorhachis*, *Parioxys*, *Fayella*, *Ecolsonia*). Changes in the proportions of central elements cannot be explained without an understanding of their functions. Plausible hypotheses regarding temnospondyl centrum function have been proposed (*vide infra*) but none of them sheds light on the amphibamid morphological shift.

The vertebral construction of dissorophoids conforms to the same type as *Eryops*, which was most recently described by Moulton (1974). The more distantly related *Edops* also has centra of this type (Romer and Witter 1942). Dissorophoids differ from these two genera in having well ossified central elements, despite their smaller size.

In lateral view, temnospondyl centra present a pattern of interlocking, alternating triangles. The ventral triangles, with points directed dorsally, are the lateral parts of the intercentra. In *Eryops*, the dorsal triangles are composed of neural arch bases and pleurocentra. The rhombic pleurocentra occupy the posterior faces of the parachordal portions of the neural arches, and their anteroventral faces continue the line of the anterior side of the arch down between adjacent intercentra (Fig. 40).

A second common type of temnospondyl centrum is that of typical trimerorhachoids. A well-described example is that of *Neldasaurus* (Chase, 1964). The pattern of interlocking triangles is more obvious in this type of column, because the neural arch bases participate little in covering the notochord. The intercentra and pleurocentra alone form the alternating wedges that make up most of the short trimerorhachoid centra. In *Trimerorhachis* itself, the intercentrum is enlarged, and the pleurocentra small and dorsally positioned (Case, 1935), but the absence of parachordal processes renders it as a *Neldasaurus*-type.

Vertebrae of *Neldasaurus* type are described for *Zatrachys* (Langston, 1953). In *Zatrachys*, the centra are not anteroposteriorly compressed, as they are in trimerorhachoids. In lateral view the central elements are triangles rather than wedges. The difference in proportions may be due to the terrestrial

habitat of the zatrachydids (Paton, 1975). Similar vertebrae are described for *Stegops* (Steen, 1938: fig. 45).

Panchen (1967) presented a complete theory of the parts of compound vertebrae. Divisions between central elements must be oblique to keep them at right angles to the plane of the rib heads. This is necessary so that the rib heads could effectively tie each neural arch to its intercentrum, thus stabilizing the vertebra. The plane of the rib heads is oblique to permit the ribs to rise in breathing movements.

Under Panchen's scenario, adaptive change produced varied kinds of vertebrae from a primitive temnospondylous one. Pleurocentrum-dominant vertebrae would develop in terrestrial animals that need strength in the vertebral column, because it is this element that supports the neural arch. Intercentrum-dominant vertebrae would develop in aquatic animals and reflect the increased importance of the axial muscles in locomotion, because the intercentra support the myocommata. Panchen (1977) later declared his hypothesis compromised by the continued lack of evidence for phylogenetic connection between the temnospondyls and other lines of tetrapods.

Within the temnospondyls, Panchen's theory seems to have explanatory value. The relatively large size of *Micromelerpeton*'s intercentra can be accounted for as due to its aquatic habitat. Likewise, the theory could be the right explanation for the large pleurocentra of such amphibamids as *A. grandiceps*, *T. texensis* and *Doleserpeton*. With regard to the origin of the amphibamid centrum, the picture is much less clear. The Panchen scenario can account for its initiation, but not for its stability. At least one line of amphibamids retained its characteristic centrum until the time of *Micropholis* in the Triassic with no further enlargement of the pleurocentrum.

Thomson and Bossy (1970) provide a commentary on vertebral morphology in their paper on trends in early amphibians. They observe that in aquatic labyrinthodonts, the divisions of the centrum are vertical rather than oblique, and that the centrum as a whole is shorter than in terrestrial forms. An example of an aquatic trend is the *Neldasaurus* type of vertebra seen in trimerorhachoids.

The first step toward an aquatic adaptation is lengthening of the plurocentra. The amphibamid pleurocentrum could have originated during an aquatic interlude in an unknown ancestor. Terrestrial life must have been resumed early under this hypothesis, because the change did not go far, and the family as we know it is basically terrestrial. However, this explanation is consistent with the shortened ribs of amphibamids. Long bony ribs are expectable in tetrapods that live subaerially, because of their use in aspiration breathing (Gans, 1970; Romer, 1972). The loss of long ribs in amphibamid ancestry left them dependent on the less efficient larval method of buccal pumping to eliminate carbon dioxide.

From his reconsideration of *A. grandiceps* and *Doleserpeton*, Bolt (1979) generated another origin hypothesis. These two species are distinguished by a lissamphibian type of dentition and enlarged pleurocentra. His scenario traces the origin of some or all modern amphibians from a terrestrial dissorophoid ancestor via a "protolissamphibian" stage exemplified by these two species. Under long-term *r*-selection, the lissamphibian lineage achieved a small body size through progenesis, one of the two mechanisms of paedomorphism. Long pleurocentra, like short ribs, are thus considered a larval or juvenile character that appeared in these fossil species when ossification occurred earlier in ontogeny than in that of their ancestors. The earlier in life the ossification took place, the more dominant the pleurocentra would be in the adult.

Bolt's hypothesis can be applied to the origin of the family as a whole, if it derived from an ancestor just paedomorphic enough to have ventrally extended pleurocentra. Short ribs are accounted for, through a selection mechanism that does not require that they be adaptive. However, Boy (1985) observes that there is no material evidence for ontogenetic change in the shape of central elements. Only the extent of ossification has been seen to change with advancing maturity.

A more recent effort to explain the temnospondyl vertebra comes from Holmes (1989). The prezygapophyses of such vertebrae face anteriorly as well as medially, and the postzygapophyses face posteriorly and laterally to match. Because of this construction, whenever the column flexed laterally it simultaneously underwent a degree of torsion. This caused sideslip along the oblique planes of the

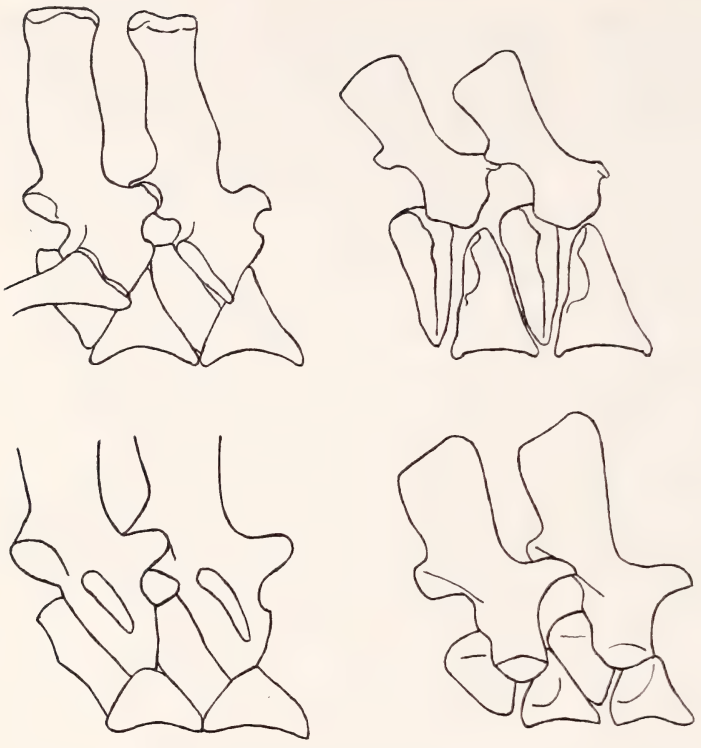

Fig. 40. Dorsal vertebrae of representative temnospondyls in right lateral view, anterior to the right. Upper left: *Eryops* vertebrae including cartilage areas as restored by Moulton 1974. Upper right: *Neldasaurus* vertebrae after Chase 1965. Lower left: *Cacops* vertebrae after Williston 1910, a variant of the *Eryops* type. Lower right: *Zatrachys* vertebrae after Langston 1953, a variant of the *Neldasaurus* type. Upper examples × 1, lower × 1.5 and 1.25.

temnospondyl centrum. The function, then, of the many parts of the centrum was to disperse the torsion along the column, so that it could twist without injury. If this analysis is correct, the mechanism remains in place in amphibamids. Their prezygapophyses all face anteriorly and their intracentral divisions are oblique.

This section should conclude with a recommendation regarding which hypothesis is most probable, but that is not possible. Instead, yet another one will be presented. The amphibamid dorsal column most closely resembles the caudal column described for certain temnospondyls: *Eryops* (Moulton, 1974), *Ecolsonia* (Berman et al., 1985), *Acheloma* (Williston, 1909) and *Phonerpeton* (Dilkes, 1990). In these tails, as in the amphibamid trunk, the pleurocentra are enlarged and extend far ventrally, almost meeting below the notochord. It appears as if caudal centrum morphology has been extended anteriorly in amphibamids. The short ribs of amphibamids could also be a manifestation of the caudal alteration.

Understanding the amphibamid centrum adaptation, then, may be through the caudal one of other temnospondyls. Typical temnospondyls were tail swimmers when in water, because their short backs and flat ribs do not allow for anguilliform movement. Their tails were flattened and undulated laterally in swimming, and probably performed an alternating torsion simultaneously, as asymmetrical tails do.

Based on this hypothesis, the amphibamid centrum is an adaptation for greater flexibility than is provided in the *Eryops* type of column of other dissorophoids. It may be indicative of aquatic ancestry, but not necessarily so. Possibly the ancestor was an exceptionally light dissorophoid, allowing the loss of some load-bearing capacity in the dorsal column in favor of greater range of motion.

The development of the gastrocentrous *Doleserpeton* vertebra may be part of another adaptive trend, perhaps back toward more support in the trunk. If this is so, the adoption of a reptile-type centrum in a temnospondyl must reflect an inability to revert to the ancestral *Eryops* centrum once it had been lost. Such a reversion has never been observed, perhaps because of both the complexity of this type of centrum, and the absence of the unique preconditions that existed when it arose.

SUMMARY

A new dissorophoid amphibian is abundant in Hamilton Quarry, an Upper Pennsylvanian locality of Kansas. It is described herein and given the name *Eoscopus lockardi,* in honor of Walter Lockard, who discovered the quarry. Four other North American dissorophoids, two species of *Amphibamus* and two of *Tersomius,* are redescribed, because of their similarities to Eoscopus. These three genera and *Doleserpeton* belong together in the family Amphibamidae, distinct from other dissorophoids by the possession of two apomorphic characters: long pleurocentra, extending to the ventral side of the centrum, and short ribs posterior to the shoulder region. These diagnostic characters are found together in two other dissorophoids: *Micropholis* from the South African Triassic, and *Micromelerpeton* from the European Lower Permian. These taxa most probably belong in the Amphibamidae. Two other aquatic dissorophoids, *Limnogyrinus* and *Branchierpeton,* also may well be amphibamids. Members of Boy's Branchiosauridae are not amphibamids and most probably not dissorophoids.

Results of analysis indicate that the nearest relatives of the Dissorophoidea are the Zatrachydidae and the Stegopidae. Eryopids and branchiosaurs are more distantly related. Within the superfamily, the Amphibamidae represent a more primitive offshoot than the Trematopidae and Dissorophidae. *Platyhistrix* and *Ecolsonia* are no longer considered dissorophids. The family Dissorophidae can be divided into two lines, one the dissorophines of DeMar, and the other based upon the genus *Cacops.*

The distinctive amphibamid vertebra is a simple derivative of the type of temnospondylous vertebra seen in *Eryops* and *Dissorophus.* The adaptive significance of this amphibamid vertebral type and that of the short ribs, is probably to attain greater flexibility than is provided in the more primitive morphology. Shortening of the ribs required the loss of aspiration breathing and constrained the amphibamids and their terrestrial descendants to a relatively small body size. The primitive form apparently could not be regained once lost.

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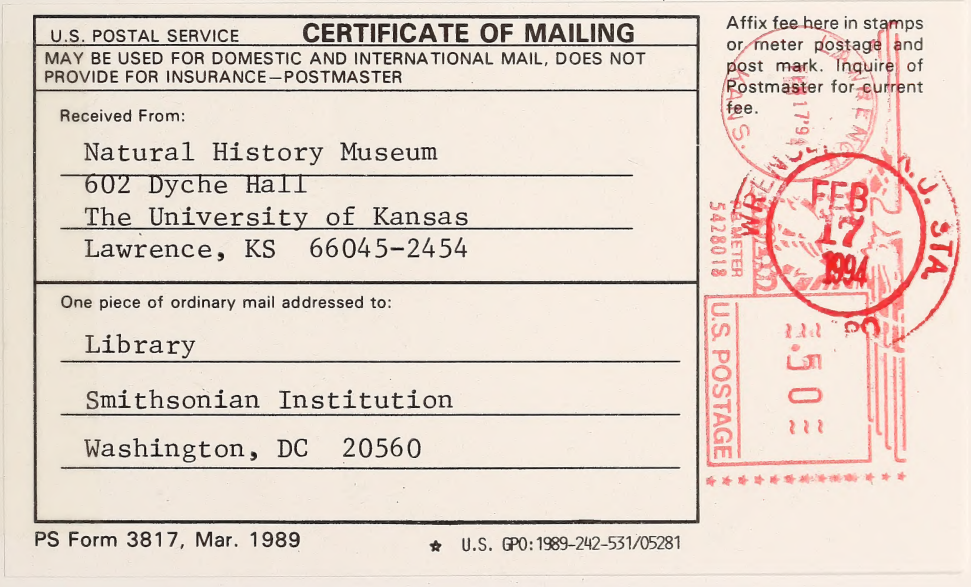

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